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OVERWINTERING OF CERTAIN CEREAL PATHOGENS IN ALBERTA¹

By W. R. FOSTER² AND A. W. HENRY³

Abstract

Helminthosporium sativum, *Fusarium culmorum*, *Ophiobolus graminis*, *Leptosphaeria herpotrichoides*, *Wojnowicia graminis*, *Erysiphe graminis*, *Tilletia caries*, and *Tilletia foetens* readily overwinter under natural conditions at Edmonton, Alberta, Canada. The first five of these overwinter at Edmonton in both spore and vegetative stages and are highly resistant to cold. Even in a non-hardened condition several of them survived severe frost. Young germ tubes of *H. sativum* for instance continued growth after being frozen solid overnight. Fresh agar cultures of *H. sativum*, *F. culmorum* and *O. graminis* grew vigorously after exposure to sub-zero temperatures. Agar cultures of *H. sativum* and *F. culmorum* were viable after a 17-day exposure to temperatures ranging from about 0° F. to -50° F.

Conidia of *H. sativum* proved less resistant to freezing and thawing than to continuous freezing. They survived longer than conidia of *F. culmorum* and *F. graminearum*. Mycelia of all foot-rot fungi grown on sterilized barley seeds were viable in one case after three months of continuous freezing, and in another after 40 alternate freezings and thawings. *H. sativum* and *F. culmorum* growing in soil survived 61 alternate freezings and thawings.

H. sativum, *F. culmorum* and *L. herpotrichoides*, retained their viability more readily on the soil surface than when buried at depths of from 2 to 12 in. Well aerated soil seemed to favor the survival of *H. sativum*, although other factors besides aeration probably are involved. Strains of *H. sativum* from high latitudes were not better adapted to low temperatures than strains from lower latitudes.

The bunt fungi, *T. caries* and *T. foetens*, are shown to be capable of overwintering at Edmonton in the form of mycelia in winter wheat. Infection of winter wheat from soil-borne spores may occur in western Canada, but in these experiments soil-borne spores did not survive to infect wheat in the spring.

Erysiphe graminis overwinters in the perithecial stage at Edmonton. In the studies made, ascospores were differentiated in the spring, when favorable conditions prevailed and before the first infections of winter wheat were observed.

Introduction

It is important to know in what form and under what conditions plant pathogenic organisms overwinter. There is little specific information of this sort about pathogens affecting crop plants in western Canada, where winters are as severe as in any other large wheat-growing area of the world. Plant pathogens may overwinter in vegetative or reproductive stages or in both, in or on the soil, the seed, living plants, or plant residues.

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Contribution from the Department of Field Crops, University of Alberta, with financial assistance from the National Research Council of Canada.

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The following pathogens were studied in these investigations:—

A. Foot-rot fungi:—

Fusarium culmorum (W. G. Sm.) Sacc., *Fusarium graminearum* Schwabe, *Helminthosporium sativum* P. K. & B., *Leptosphaeria herpotrichoides* De Not.*, *Ophiobolus graminis* Sacc., *Wojnowicia graminis* (McAlp.) Sacc. & D. Sacc.*

B. Bunt or stinking smut fungi:—

Tilletia caries (D.C.) Tul., *Tilletia foetens* (Berk. & Curt.) Trel.

C. Powdery mildew fungus:—

Erysiphe graminis D.C.

Overwintering of Fungi Causing Foot Rots and Other Diseases

LITERATURE REVIEW

The foot rot and seedling blight of wheat caused by *Fusarium* spp. develops, according to Dickson (6), from two main sources, infected seed and infested soil. Henry's results (12) indicate that in Minnesota the mycelium and possibly some of the spores of *Fusarium* spp. overwinter on debris in the soil or on its surface. Atanasoff (2) states that species of *Fusarium* are remarkably resistant to desiccation and low temperatures and assumes that they overwinter in winter crops as mycelium, conidia and chlamydospores.

Henry (12) found that a rather large proportion of conidia of *Helminthosporium sativum* overwintered on debris in the soil or on its surface at St. Paul, Minnesota. Christensen's results (3), also obtained at St. Paul, Minnesota, indicate that mycelia and spores of *H. sativum* overwinter in the field on old straw, roots, seed, and in the remains of grasses.

Ophiobolus graminis, the fungus that causes the destructive "Take-all," was found by Kirby (15) in New York State, and by Davis (5) in Wisconsin, to overwinter in both ascospore and mycelial stages. Kirby found that winter wheat was damaged most and he considered that the organism lived over the winter on infected plants.

Leptosphaeria herpotrichoides, found in Alberta by Henry and Foster (13), is favored by a mild damp winter in France according to Guyot (10).

OVERWINTERING OF FOOT ROT FUNGI UNDER NATURAL CONDITIONS ON CROP RESIDUES

Overwintered wheat stubble from fields badly diseased with foot rot was collected. Spores of three of the foot-rot fungi, namely, *Leptosphaeria herpotrichoides*, *Ophiobolus graminis* and *Wojnowicia graminis* were present on some of the collections. These were tested for germination in Van Tieghem cells. Pieces of stubble from the various collections were surface sterilized and plated on potato-dextrose agar to determine the viability of any mycelium

* Weakly pathogenic as compared with the others.

present in them. The fungi that developed were checked for identity with monosporous known cultures of the various foot-rot organisms on the same medium.

The mycelium of all organisms mentioned in Table I survived the winter on wheat stubble. A few of the ascospores of *L. herpotrichoides* and pycnosporos of *W. graminis* were viable in the spring but positive results with the ascospores of *O. graminis* were not obtained. However, Davies (4) has since shown that the ascospores of *O. graminis* overwinter at Edmonton. No conidia of *H. sativum* and *F. culmorum* were observed on the stubble examined but, as is shown later, these readily overwinter here.

TABLE I
SURVIVAL OF FOOT-ROT FUNGI UNDER NATURAL
CONDITIONS ON WHEAT STUBBLE DURING
THE WINTER OF 1928-29

Fungus	Isolation of mycelium	Spore germina- tion
<i>Fusarium culmorum</i>	+	—
<i>Helminthosporium sativum</i>	+	—
<i>Leptosphaeria herpotrichoides</i>	+	+
<i>Ophiobolus graminis</i>	+	—
<i>Wojnowicia graminis</i>	+	+

+ Spores and mycelium viable.
— no spores viable.
— No tests made.

COLD RESISTANCE UNDER ARTIFICIAL CONDITIONS

Under natural conditions, pathogenic fungi probably harden off in the same way as higher plants with the gradual onset of cold weather. They also cease growth, and frequently go into dormant or resistant stages. Hence it might be expected that they would survive freezing more readily under such conditions than if kept previous to freezing in a warm atmosphere. In order to test the cold resistance of foot-rot fungi in what would seem to be their most vulnerable states, experiments were made with freshly germinated spores and with fresh agar cultures grown in the laboratory at room temperature.

Effect of Freezing on Young Germ Tubes

In order to determine the resistance of young germ tubes to freezing, spores of *H. sativum* were chosen and germinated in water in Van Tieghem cells. When the germ tubes were from one to three times the length of the spores, the cells were placed outside overnight at freezing temperatures. The minimum temperature reached during exposures was 6° F. The drops of water containing the spores were of course frozen solid. In the morning the cells were returned to the laboratory where the ice soon melted. By the use of several microscopes a number of the germinated spores were then kept under observation to determine the behavior of their germ tubes following freezing. With the aid of a camera lucida a few typical germinated spores were drawn before and after freezing. Some of these are illustrated in Fig. 1.

As Fig. 1 shows, freezing did not kill the germ tubes or injure them severely, though it did tend to induce lateral branches and the formation of new germ

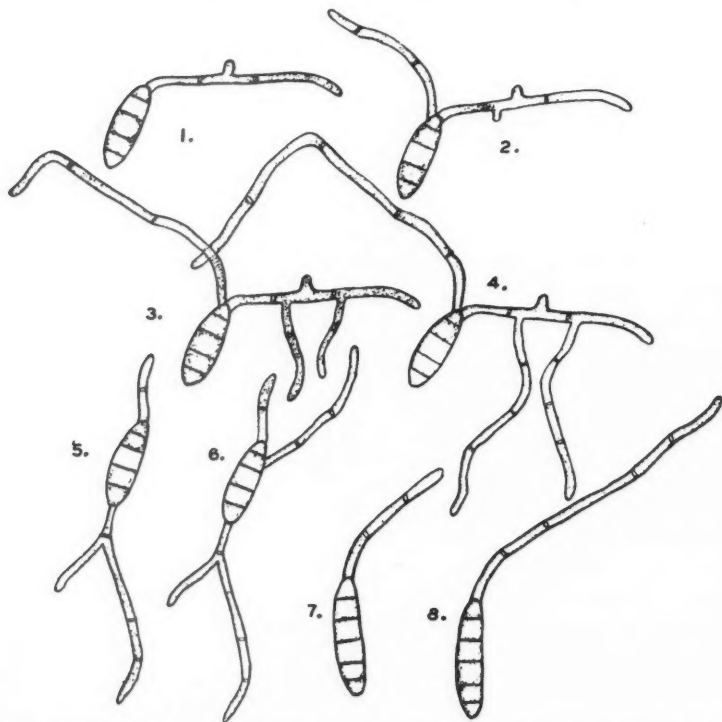


FIG. 1. Effect of freezing fresh germ tubes of *Helminthosporium sativum* in ice over-night. 1-4. Different stages of one germinated spore before and after freezing. No. 1 shows the stage at which freezing took place; 2-4 show stages of growth after thawing. 5-6. No. 5 shows the stage at which another germinated spore was frozen and No. 6 one stage of growth after thawing. 7-8. No. 7 shows the stage at which a third germinated spore was frozen and No. 8 shows the same germinated spore later when the germ-tube had elongated by growth from the tip.

tubes, indicating some damage to the growing tips. However, continuation of new growth from the tip was observed in a few cases. Similar results were obtained with *Fusarium culmorum*.

Effect of Freezing on Growing Cultures on Agar

In order to test the ability of *H. sativum*, *F. culmorum* and *O. graminis* to survive freezing when in a growing condition, potato-dextrose-agar cultures grown in glass test tubes, in the laboratory at room temperature, were exposed outside to freezing temperatures and tested for viability immediately after thawing. If growth was resumed following transfer to fresh slants of potato-dextrose agar, of portions of colonies that had been frozen, tests were considered positive.

Test No. 1. Cultures of *H. sativum* and *F. culmorum*, about a week old, were placed outside on a window ledge overnight. The minimum tempera-

ture reached during the night was 17° F. The cultures were taken into the laboratory at 9 a.m. next morning, allowed to thaw and then tested for viability. Both fungi grew vigorously after this exposure.

Test No. 2. Cultures of *H. sativum*, *F. culmorum* and *O. graminis*, approximately two weeks old, were exposed outside for two hours in a thermograph box about 1½ ft. above the surface of the ground. The thermograph registered -4° F. at the beginning and 0° F. at the end of the exposure. All three fungi grew well after this exposure to below-zero temperatures.

Test No. 3. Cultures of *H. sativum*, *F. culmorum*, and *O. graminis*, 26 days old, were put outside in the same position as the cultures in Test 2, and left there for a period of 3½ days. The temperature was -29° F. at the beginning of the exposure and continued below zero throughout, gradually rising to -1.5° F. at its termination. Tests for viability after the exposure were positive for all three fungi.

Test No. 4. For this test, month-old cultures of *H. sativum* and *F. culmorum* were used. They were placed outside in the same position as the cultures in Tests 2 and 3, at 9.30 a.m. Feb. 4, 1936, and remained there until 3 p.m. on Feb. 21, 1936, when they were returned to the laboratory, allowed to thaw, and tested for viability. The period chosen for this test happened to be one of exceptionally prolonged cold weather (see Table II). For

TABLE II

MAXIMUM AND MINIMUM AIR TEMPERATURES (°F.) RECORDED IN THE OPEN AT THE UNIVERSITY OF ALBERTA DURING FEBRUARY, 1936

	Record A*		Record B*		Record C*	
	max.	min.	max.	min.	max.	min.
Feb. 4	-18	-45	-4	-40	-18.5	-39
5	-19	-43	-14	-38	-20	-38.5
6	-29	-39	-14	-30	-29	-36
7	-24	-47	-22	-42	-30	-41.8
8	-15	-43	-14	-30	-17	-31
9	-15	-24	-2	-18	-15.5	-19
10	-13	-21	0	-20	-14	-23
11	-15	-33	-4	-29	-13.5	-19
12	-14	-41	-2	-39	-9.5	-36
13	-14	-43	-2	-38	-12	-42
14	-22	-41	-8	-36	-21	-38.8
15	-23	-50	-13	-46	-14	-45.5
16	-17	-56	-10	-50† (?)	-21	-51
17	-12	-45	-4	-26	-9.5	-26.7
18	-10	-38	+2	-34	-5.5	-36
19	-4	-34	+7	-20	-3	-23.5
20	-2	-24	0	-20	-1.5	-23
21	+1	-20	+17	-11	+3	-13

*Record A. Max. and min. thermometer, Experimental Plots, Field Crops Dept., University of Alberta, Edmonton. (Courtesy Mr. J. W. Hopkins).

Record B. J. P. Fries thermograph, University of Alberta Campus, near West Lab. †estimated—open below chart.

Record C. Max. and min. thermometer, University of Alberta Campus, near North Lab., Dept. of Civil Engineering. (Courtesy Prof. H. Webb).

instance, a minimum temperature of at least -50°F . was recorded at the University by two maximum and minimum thermometers and a thermograph, on the night of Feb. 16, and the temperature was consistently below zero for most of the period. *H. sativum* and *F. culmorum*, however, grew vigorously following the exposure.

The results of these tests clearly demonstrate that non-hardened cultures of *H. sativum*, *F. culmorum* and *O. graminis* are highly resistant to low temperatures. Under natural conditions these fungi are not likely to be exposed to such severe conditions. In most situations where they occur, for instance, on stubble and other crop residues, they are covered during much of the winter by a protective blanket of snow. Moreover, under natural conditions, they would usually have an opportunity of becoming more resistant to cold owing to a hardening process in the fall. Hence if these organisms can survive the above conditions, it might be expected that they would be successful, as has been demonstrated, in overwintering under natural conditions.

Effect of Continuous and Alternate Freezing and Thawing

During an Alberta winter, organisms under outside conditions may be exposed to wide variations in temperature both above and below the freezing point. If there is no protective cover, the fluctuations will be especially wide, particularly in the spring or during occasional warm periods or "chinnooks." On the other hand, if the organisms are under snow, soil, or other cover, they will sometimes be exposed to less extreme and relatively constant temperatures for long periods.

In order to determine the relative effects of continuous freezing and alternate freezing and thawing on foot-rot fungi, cultures on sterilized barley kernels were frozen in ice outside, and in a refrigerator at -5°C . Each morning half of the outside cultures were brought into the laboratory and allowed to return to room temperature. As soon as the ice melted they were put out to freeze again. The other cultures were kept frozen continually and tested for viability at intervals. Data were taken on both spores and mycelia.

In one experiment a culture of *H. sativum* was tested over a period of eight weeks. A portion of it was kept frozen solid during this period while the remainder was frozen and thawed forty times. The results of viability tests of representative samples of this material are given in Table III.

It will be noted from the above table that intermittent freezing killed the spores of *H. sativum* more rapidly than did continuous freezing. The conidia survived twice as long when kept frozen as they did when frozen and thawed almost daily. In this connection, Christensen (3) found that conidia of *H. sativum* survived freezing and thawing in water for a considerable time. The mycelium in the above experiment evidently survived after the spores were killed, as it was viable in all tests as indicated by positive results throughout the vegetative growth. This may have been due to its presence within the barley kernels where it may have been less subject to injury than on the surface.

TABLE III

EFFECT OF CONTINUOUS AND INTERMITTENT FREEZING ON THE VIABILITY OF *H. sativum* GROWN ON STERILIZED BARLEY SEEDS

Periods of testing	Number of times frozen and thawed	Germination of <i>H. sativum</i>			
		Continuous freezing		Intermittent freezing	
		Germination of conidia	Vegetative growth	Germination of conidia	Vegetative growth
1 day	1	High	+	High	+
3 days	3	High	+	High	+
1 week	6	High	+	High	+
2 weeks	12	High	+	Low	+
3 weeks	18	High	+	Low	+
4 weeks	24	Medium	+	0	+
6 weeks	36	Low	+	0	+
8 weeks	40	0	+	0	+

In another experiment the effect of continuous freezing of several fungi over a three month period was studied. The results of this experiment are given in Table IV.

TABLE IV

EFFECT OF CONTINUOUS FREEZING ON SEVERAL FOOT-ROT FUNGI GROWN ON STERILIZED BARLEY SEEDS

Organism	Source	1 month		2 months		3 months	
		Germ. conidia	Growth myc.	Germ. conidia	Growth myc.	Germ. conidia	Growth myc.
<i>F. culmorum</i>	Edmonton, Alta.	Med.	+	0	+	0	+
<i>F. graminearum</i>	St. Paul, Minn.	Med.	+	0	+	0	+
<i>F. graminearum</i>	Baton Rouge, La.	Med.	+	0	+	0	+
<i>H. sativum</i>	Ft. Vermilion, Alta.	High	+	Low -	+	0	+
<i>H. sativum</i>	Edmonton, Alta.	High	+	Low -	+	0	+
<i>H. sativum</i>	St. Paul, Minn.	High	+	Low -	+	0	+
<i>H. sativum</i>	Baton Rouge, La.	High	+	Low -	+	0	+
<i>L. herpotrichoides</i>	Camrose, Alta.	-	+	-	+	-	+
<i>O. graminis</i>	Camrose, Alta.	-	+	-	+	-	+
<i>W. graminis</i>	Edmonton, Alta.	-	+	-	+	-	+

*Low = 1-10%, Medium = 11-35% = 35-100%.

All the fungi included in the above experiment, namely, *Fusarium culmorum*, *Fusarium graminearum*, *Helminthosporium sativum* (four strains), *Leptosphaeria herpotrichoides*, *Ophiobolus graminis* and *Wojnowicia graminis*, survived the entire three months frozen solid continuously in ice. The spores of all four strains of *H. sativum* survived this treatment for two months, but those of the two species of *Fusarium* were dead in two months and those of *H. sativum* in three months. No spores of *L. herpotrichoides*, *O. graminis* or *W. graminis* were available for testing. Although not indicated in Table IV, all of the fungi mentioned in it also survived alternate freezing and thawing forty times during a two month period.

In another experiment *H. sativum* and *F. culmorum* were grown in sterilized soil instead of barley grains and tested in this medium for resistance to alternate freezing and thawing. In this experiment the cultures were started at room temperature in test tubes containing equal portions of the autoclaved soils, which had previously been made up to their water-holding capacity with distilled water. Three soils representative of the three main soil types of the province were used, namely, black, brown, and gray, with average organic matter contents of 10, 6 and 10. The fungi were allowed to develop in these soils for 17 days at room temperature, after which the test tubes were placed in a refrigerator at 8° C. for 11 days. Viability tests were then made, all of which were positive. Freezing and thawing was then begun. The usual procedure was to place the tubes of soil on the trays between the coils of a refrigerator at a temperature of about -5° C. and to leave them overnight. They were removed about 9 a.m. next day and allowed to remain at room temperature until 5 p.m., when they were again placed in the refrigerator and frozen. They were not melted every day, but on the average on each of about 15 days a month over a period of about four months. In all, the cultures were frozen and thawed 61 times, after which viability tests were made. These were positive for both fungi in each of the soil types. The treatments were not continued, so it is not possible to say how long the fungi will survive such exposures. It is clear, however that they are not readily killed in sterilized soil by alternate freezing and thawing.

LOCATION IN THE SOIL IN RELATION TO WINTER SURVIVAL

Christensen (3) has reported that aeration is an important factor in prolonging the life of conidia of *H. sativum*. This might be one of the factors affecting the survival of organisms deposited in the soil. Aeration would ordinarily decrease with depth and with increasing firmness of the soil. Hence winter survival at different depths in the soil or in soils of varying degrees of firmness might vary because of differences in air supply.

In order to ascertain whether position in the soil and firmness of the soil have any effect on the overwintering of foot-rot fungi, barley seed cultures were placed outside on the surface of Edmonton black soil and also at depths of 2, 4, 8 and 12 in., on November 1, 1928, *Helminthosporium sativum*, *Fusarium culmorum* and *Leptosphaeria herpotrichoides* were used in this experiment. Viability tests were made of the overwintered cultures May 1, 1929. The results of these tests are given in Table V.

The data in Table V indicate that all three fungi survived better on the surface than below ground. The conidia of *H. sativum* kept on the surface also germinated better than those from below ground, though this was not true of *F. culmorum* spores. *H. sativum*, overwintered in unpacked soil, also showed a higher degree of viability than that overwintered in packed soil; but no difference was shown by either *F. culmorum* or *L. herpotrichoides*. In another experiment in which barley seed cultures of *H. sativum* and *F. culmorum* were overwintered in different types of soil, those kept in sand, the

TABLE V
EFFECT OF EXPOSURE OUTSIDE DURING THE WINTER OF 1928-29 OF CULTURES OF
FOOT-ROT FUNGI AT DIFFERENT DEPTHS, AND IN PACKED AND UNPACKED SOIL

Treatment	Germination of conidia*		Growth on agar		
	<i>H. sativum</i>	<i>F. culmorum</i>	<i>F. culmorum</i>	<i>H. sativum</i>	<i>L. herpotrichoides</i>
<i>Depths of inoculation</i>					
Surface	High	Low	Excellent	Excellent	Good
2 in. below	Low —	Medium —	Fair	Poor	Fair
4 in. below	Low —	Low	Fair	Poor	Fair
8 in. below	Low —	Low	Fair	Poor	Fair
12 in. below	Low +	Low	Good	Fair	Fair
<i>Firmness</i>					
Packed 4 in.	Low	Low	Fair	Poor	Fair
Unpacked 4 in.	Medium	Low	Fair	Fair	Fair

* Low = 1-10%; Medium = 11-35%; High = 36-100%.

most porous soil, showed a higher percentage germination of their conidia than any of the others. It would appear therefore that good aeration may be a factor favorable to successful overwintering. The above experiments, however, provide no conclusive proof of this. It is possible, for example, that differences in the amount of moisture, and in the activity of soil micro-organisms at different levels, might affect the survival of the pathogenic fungi under consideration.

ECOLOGICAL ADAPTATION

The ability of an organism to overwinter in northern regions might conceivably be due to the occurrence of specially cold-resistant strains in those areas. In order to test this hypothesis, strains of *H. sativum* were obtained from a number of points from Fort Vermilion, Alberta, in the north, to Baton Rouge, Louisiana, in the south. These cultures were grown on potato-dextrose agar and exposed to temperatures ranging from 5° to 35° C. and their reactions measured by taking the average diameters of the colonies.

TABLE VI
REACTION OF DIFFERENT STRAINS OF *Helminthosporium sativum* TO
DIFFERENT TEMPERATURES

Source of strains of <i>H. sativum</i>	Diameter of colonies in millimeters at various temperatures						
	5° C.	10° C.	15° C.	20° C.	25° C.	30° C.	35° C.
Fort Vermilion, Alberta	11	15	47	62	88	62	25
Berwyn, Alberta	11	18	32	41	48	76	14
Edmonton, Alberta	11	18	23	49	85	86	25
Ohaton, Alberta	12	15	54	71	88	86	26
Calgary, Alberta	16	23	46	69	88	77	18
Brooks, Alberta	17	25	32	46	72	65	15
Claresholm, Alberta	14	25	45	61	87	60	15
St. Paul, Minnesota	14	18	37	64	75	76	16
Baton Rouge, Louisiana	8	13	30	46	52	58	0

The data presented in Table VI do not indicate that northern strains grow better at lower temperatures than do those from points farther south. The responses of the different strains to temperatures seem to be about the same. The Berwyn and Baton Rouge strains appear to have a slightly higher optimum than the others. Four of the above strains from latitudes ranging from Fort Vermilion, Alberta, to Baton Rouge, Louisiana, reacted similarly to continuous freezing and to alternate freezing and thawing. No definite ecological adaptation is therefore demonstrated in these experiments.

Overwintering of Bunt Fungi

LITERATURE REVIEW

The bunt fungi are known to overwinter commonly in western Canada in the form of chlamydospores adhering to the surface of the seed. There has, however, been a lack of experimental evidence, to show whether the bunt fungi can survive the winter as mycelia in winter wheat in western Canada. Woolman and Humphrey (16) have demonstrated that soil-borne spores may cause a smutty crop of wheat in the Palouse region of Idaho, Washington and Oregon, even though the seed has been carefully treated. However, when spring wheat is sown on similarly infested soil the crop remains practically bunt free, indicating that the spores do not survive the winter in that region. Appel and Riehm (1) and others have also reported the failure of free spores to overwinter. In western Canada, Cüssow and Conners (9) point out that "As a rule threshing is done so late in the fall the soil is too cold to permit the germination of any spores which have been set free by this operation." They call attention, however, to the effectiveness of seed treatments in controlling bunt of spring wheat and consider that this indicates that infection from spores which have overwintered in the soil does not commonly occur. Hanna and Popp (11) found that bunt spores (*Tilletia caries*) in infected heads of Mindum wheat placed on the surface of the ground overwintered successfully at Winnipeg, Morden, Brandon, Indian Head, Saskatoon and Edmonton, in western Canada.

EXPERIMENTAL RESULTS

On September 6, 1928, field plots were laid out at Edmonton, and bunt spores were distributed both in rows and broadcast. Treated and non-treated Kharkov winter wheat were seeded in half of the plots. On April 26, 1929, the remaining half was sown to Marquis wheat. Temperature and moisture conditions were favorable for infection both in the fall and spring. When the grain was nearly mature the percentage of bunted heads was recorded and specimens collected to determine the species that overwintered.

Table VII shows that winter wheat sown in the fall in soil infested with bunt spores became affected with bunt, while spring wheat did not. Soil-borne spores of both *Tilletia caries* and *Tilletia foetens* caused infection of winter wheat. The bunt spores evidently did not survive the winter in the soil, but the mycelium in winter wheat plants readily overwintered. It is

TABLE VII
EFFECT OF SOIL INFESTATION WITH CHLAMYDOSPORES ON THE DEVELOPMENT
OF BUNT IN WINTER AND SPRING WHEAT

Seed treatment	Soil treatment	Winter wheat Heads infected, %	Spring wheat Heads infected, %
Check	No inoculum	0.0	0.0
Untreated	Inoculum added to rows	14.0	0.0
Copper carbonate	Inoculum added to rows	9.7	0.0
Formaldehyde	Inoculum added to rows	10.0	0.0
Hot water	Inoculum added to rows	10.0	0.0
Check	No inoculum	0.0	0.0
Untreated	Inoculum broadcasted	13.5	0.0
Copper carbonate	Inoculum broadcasted	8.5	0.0
Formaldehyde	Inoculum broadcasted	10.7	0.0
Hot water	Inoculum broadcasted	10.0	0.0

also of interest to note that the infection of winter wheat was practically as great in the plots where the spores were broadcasted as in those in which the spores were deposited in the seed rows. There seems, therefore, to be a good possibility of winter wheat becoming infected with bunt in Alberta from soil-borne spores. Seed treatment, as shown by Table VII, will not prevent this type of infection. The greater prevalence of bunt in winter wheat as compared with spring wheat in Canada, may be accounted for by the above results. According to estimates of the Board of Grain Commissioners of Canada, winter wheat in Canada had proportionally about 70, 50 and 18 times as much bunt as spring wheat in 1926, 1927 and 1928. Furthermore, contrary to the suggestions of Güssow and Connors (9), fall conditions at threshing time and after are often favorable for germination of bunt spores. The mean monthly air temperature for September at Edmonton for the last 47 years was 50° F. According to Hungerford (14), Gibs (7), Güssow and Connors (9) and others, maximum infection takes place between 46° and 50° F. Further, the average soil temperature two inches below the surface for the last three weeks in September, 1928, was even somewhat higher than the optimum soil temperature for infection.

It appears that temperature conditions in the fall at Edmonton are generally favorable for infection of winter wheat from soil-borne bunt spores.

Overwintering of the Powdery Mildew Fungus of Wheat

Erysiphe graminis D.C., the fungus causing powdery mildew of grasses, occurs commonly in the moister parts of Alberta on wheat and rye as well as on many wild and cultivated grasses. Winter wheat and winter rye are usually the cereals most heavily attacked, but spring wheat is frequently and sometimes quite severely affected. Powdery mildew has not been observed at Edmonton in the field on oats and barley, though the disease developed on oats in the greenhouse on one occasion.

Both conidial and perithecial stages of *Erysiphe graminis* develop in abundance at Edmonton on affected plants. In order to determine whether the fungus overwinters on wheat in either or both of these stages, the behavior of

TABLE VIII
VIABILITY OF CONIDIA OF *Erysiphe graminis* FROM WINTER WHEAT COLLECTED IN THE FALL OF 1928

Date of collection	Germination of conidia, %
Oct. 1	11
Nov. 1	0
Dec. 1	0

each was followed during the fall, winter, spring, and early summer of 1928-29.

Collections of conidia from winter wheat were made at monthly intervals during the fall. These were brought to the laboratory and tested for germination on the day of collection. The results of the tests are given in Table VIII.

It will be seen that viable conidia were present on winter wheat on Oct. 1, but after that no germination occurred. The conidia not only failed to germinate in the late fall but were difficult to find, which suggests that they are not concerned in the overwintering of the fungus here.

Perithecia were also collected from winter wheat during the fall of 1928 and at various times thereafter up to June 15, 1929. Diseased leaves were brought to the laboratory at each date of collection and perithecia from them were crushed and examined under the microscope for the presence of asci containing mature germinable ascospores. As is indicated in Table IX, no perithecia having asci with differentiated ascospores were found until May 15. By the second week in June numerous mature ascospores were found in the perithecia examined. The first infections of winter wheat observed in 1929 were found on June 15. Thus the maturing of the ascospores corresponded very well with the appearance of the initial infections. This, coupled with the failure of the conidia to survive after October, indicates that the fungus overwinters here in the perithecial stage.

TABLE IX
DEVELOPMENT OF ASCOSPORES OF *Erysiphe graminis* IN THE FIELD AT EDMONTON IN 1928-1929

Date	Ascospores formed
Oct. 1	—
Nov. 1	—
Jan. 3	—
Feb. 4	—
March 1	—
April 1	—
May 1	—
May 15	+
June 1	+
June 8	++
June 15	++

— No ascospores differentiated;
+ ascospores beginning to differentiated;
++ ascospores differentiated.

TABLE X
AVERAGE MAXIMUM AND MINIMUM DAILY TEMPERATURES, ° F., AT EDMONTON, BY WEEKLY PERIODS FROM MAY 1 TO JUNE 15, 1929

Week ending	Average temperatures, ° F.	
	Maximum	Minimum
May 7	55.6	29.0
14	57.7	35.9
21	66.9	37.6
28	65.6	42.0
June 4	70.9	46.9
11	78.3	47.9
18	71.9	47.3

Graf-Marin (8) has recently investigated methods of breaking the dormancy of perithecia of *Erysiphe graminis*. Best results were obtained by chilling the perithecia, immersed in water, for 12 hr. at 9° C. (48·2° F.) and then transferring them to a constant temperature of 21° C. (69·8° F.). Ascospores were then formed in 22 hr.

An examination of daily maximum and minimum temperature records at the University of Alberta, Edmonton, for May and the first two weeks of June, 1929, reveals a gradual rise during May to temperatures at the end of the month and during the first two weeks of June, closely approaching those reported as optimum for ascospore differentiation by Graf-Marin (Table X). As already noted and as may be seen in Table IX, most ascospore differentiation was actually observed on June 8 and June 15.

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THE ORIGIN OF RUSSETING IN THE GOLDEN RUSSET APPLE¹

BY HUGH P. BELL²

Abstract

About the time of full bloom, many epidermal cells divide by a tangential wall. Later in June all the epidermal cells become vacuolated and some divide again by tangential walls forming a layer varying from two to four cells thick. Early in July a cambium is initiated in the innermost cells of epidermal origin. This cambium is very active and immediately gives off cells which differentiate into cork. Non-russeted portions may have either a very thick convoluted cuticle or a double layer of cuticle. The development of the periderm and the histology of the mature protective layers are illustrated by fifteen figures.

Introduction

During the spring of 1936, the Pathologist-in-Charge at the Laboratory of Plant Pathology, Kentville, Nova Scotia, was studying the question of russetting on certain varieties of apples. His immediate problem was the pathological aspects of this phenomenon, but before a satisfactory diagnosis could be made of the pathological condition, it was considered desirable to have more information regarding russetting as it occurs normally on certain apples. The study outlined below was undertaken to obtain this information.

Historical

The development of normal russetting is described briefly by Zschokke (7). He also has a few figures illustrating its origin and development. In agreement with the findings given below, he states that the cork cambium cells arise from the inner half of epidermal cells, but his description of the histology and development is very brief and his figures are almost idealistic in their regularity of tissues and perfection of cells. Thus his article was of little assistance in identifying the tissues in the material collected at Kentville. Recent reports on russetting that arose as the result of injury describe the corky or periderm layer as originating in sub-epidermal layers. For instance MacDaniels and Heinicke (4, p. 905) state ". . . . the wound has been corked over by the activity of a periderm layer formed in living cells beneath the injured tissue." Also Clements (3) reports that in the rare cases where real cork occurs in the lenticels of the apple, it develops from the inner cells beneath the ruptured epidermis. In all these cases the mature periderm is apparently similar in structure, regardless of whether it arises normally, or as the result of injury, or in the development of a lenticel. Hence, as recent investigators agreed that the periderm of injuries and lenticels arose from inner tissues, and as the figures of Zschokke did not agree in detail with the material collected at Kentville, it was considered necessary to make a careful study of the subject. This was done not only to see whether Zschokke was

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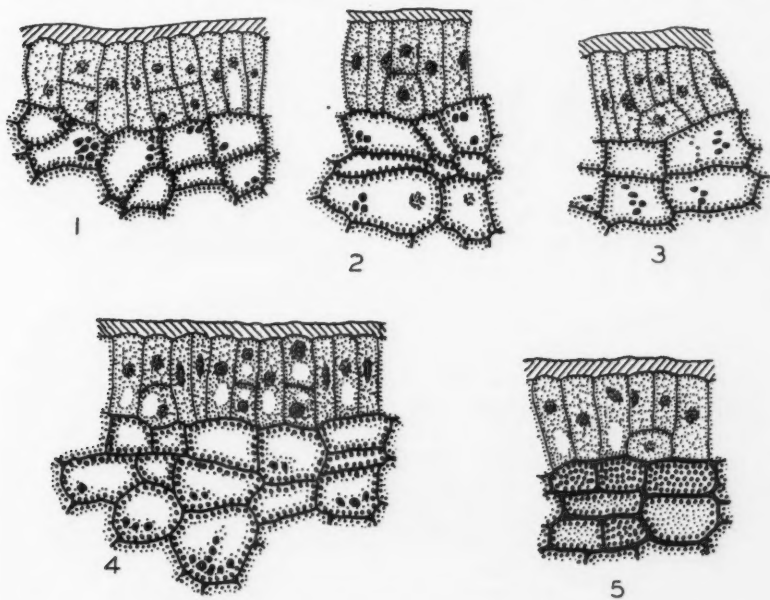
correct when he stated that normal russetting in the apple originated in the epidermis, but also to get more detailed information regarding the histology of russetting.

Material and Methods

The variety of apple used was the Golden Russet. Collections were made biweekly from normal trees in the orchard of the Experimental Farm at Kentville, Nova Scotia. The material was killed in chrom-acetic, imbedded in paraffin as described by Bell and Facey (2) and stained in safranin and fast green. The section thickness that proved most satisfactory was 6μ . Sections thicker than this were useless for accurate interpretation of tissue development. In 1936 the trees from which the material was collected were in full bloom during the last week in May.

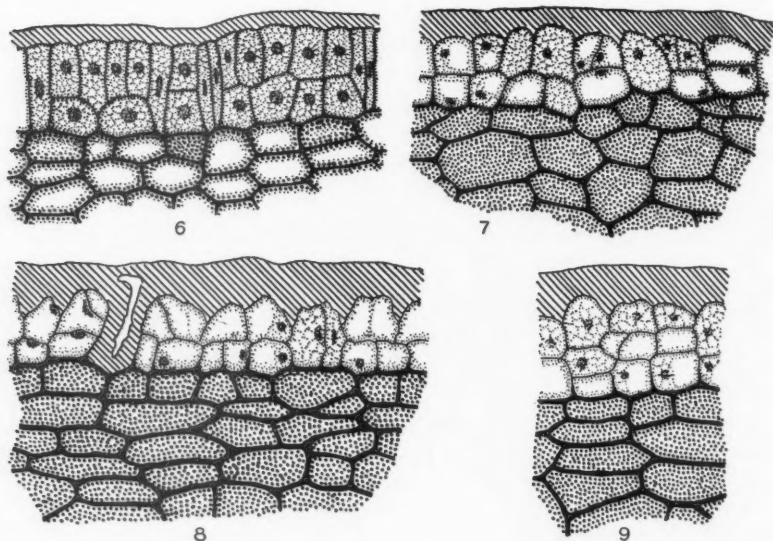
Development and Histology

Before and during full bloom, the epidermal structure of the Golden Russet is very similar to that found during the same period in the McIntosh Red. This has been described and illustrated by Bell (1). That is, at full bloom



FIGS. 1-5. Radial sections through outer layer; cuticle singly cross-hatched. FIG. 1. June 4. Three of the epidermal cells have divided by tangential walls. $\times 550$. FIG. 2. June 4. The inner half of a divided epidermal cell has broadened slightly tangentially. $\times 550$. FIG. 3. June 4. The outer half has divided by a radial wall and the inner half has broadened considerably tangentially. $\times 550$. FIG. 4. June 4. Three cells have divided transversely, and the inner half of the left hand divided cell has broadened tangentially. $\times 550$. FIG. 5. June 8. Similar to Fig. 3, but the cells have assumed a different shape. $\times 550$.

the epidermis consists of closely packed columnar cells with a radial measurement a little more than twice the tangential. The variation from the normal which gives the Golden Russet its distinctive character starts during and shortly after full bloom. It consists of tangential divisions in the epidermal cells. At first the tangential walls occur in a very few cells. In nearly all cases they are slightly nearer the inner than the outer end of the cell (Figs. 1, 4). As this transverse division becomes more common throughout the epidermis, the inner half broadens in a tangential direction (Figs. 2, 4). At the same time, the outer half frequently divides by a radial wall (Figs. 3, 5). This radial division of the outer cell obscures the origin of the inner half, and as this inner half has broadened tangentially and flattened radially, it has become quite similar in appearance to the cells of the hypodermis, and unless the earlier stages have been observed very carefully, it is very easy at this stage to make a mistake and regard the inner cell of the epidermis as sub-epidermal in origin. While this development in the epidermis is taking place, the cuticle is thickening rapidly. During the early part of June, cell division and cell differentiation continue, until by the middle of the month, nearly the whole epidermis is transformed into a layer two cells thick (Fig. 7).



FIGS. 6-9. Radial sections through outer layer; cuticle singly cross-hatched. FIG. 6. June 11. Transverse division and tangential broadening, especially of the inner cells, has extended throughout most of the epidermis. $\times 400$. FIG. 7. June 18. Most of the epidermis has been transformed into at least two layers of vacuolated cells. $\times 400$. FIG. 8. July 6. A conspicuous hair base, the inside end of which indicates quite clearly the inner boundary of the epidermal layer. $\times 400$. FIG. 9. July 6. A typical example of those regions in which there has been more than one tangential division in the cells of epidermal origin, resulting in a layer more than two cells thick. $\times 400$.

Concurrent with or immediately following the developmen : outlined above, a number of other changes occur. For instance, all the epidermal cells enlarge greatly in a tangential direction and become vacuolated. The outer cells become partially separated by V-shaped invasions of the cuticle. Either the outer or inner cells or both may divide again by a tangential wall. Thus by the first week in July, the epidermis is a layer of broad vacuolated cells. It usually varies in thickness from two to four cells and is covered by a thick and invading cuticle (Fig. 9). But it must be understood that there are still some regions in which no division of the epidermal cell has taken place and there, of course, the epidermis is still one cell thick, but these single cells are usually very large. (See fourth and fifth epidermal cells from the right, Fig. 8.)

In those places where a number of divisions have occurred and the epidermis is three or four cells thick, it has become increasingly difficult to determine with certainty where cells of epidermal origin end, and those of hypodermal origin start. The most trustworthy landmark is the inner end of the hair base. This marks the original inside boundary of the epidermis, for as the epidermis thickens and becomes multicellular, the hair base lengthens and is made conspicuous in transverse section by a heavy deposition of cuticle around the base and sides and finally over the top of this columnar cavity (Fig. 8). By using this hair base as a landmark, it is comparatively easy to determine the boundary between cells of epidermal and cells of sub-epidermal origin.

During the first two weeks in July the whole structure of the epidermal or outer protective layer differentiates very rapidly; so rapidly that it is necessary to make many collections close together to interpret the changes correctly. The exact sequence of change is obscured because in this one group of cells, growth is taking place simultaneously in two directions and by two very different methods. So different are these two methods that they appear to conflict with each other, and yet they are progressing concurrently in the same group of cells. First the ovary is enlarging very rapidly and the outer protective layer must accommodate itself to this enlargement by growth in a tangential direction. To accomplish this the cells stretch tangentially, flatten radially, occasionally divide by a radial wall, and are all displaced and more or less distorted. Many, especially the outer ones, become crushed or even ruptured. This phase of the differentiation is accomplished chiefly by stretching and gliding growth. While this tangential extension, with the consequent distortion and disruption of cells, is progressing, a regular cork cambium layer is being differentiated and cork cells are being cut off and pushed out radially. This phase of the growth is accomplished by rejuvenation of vacuolated cells into meristematic cells, followed immediately by rapid growth in a radial direction; the latter, of course, being the result of cell division in which the new dividing walls are laid down tangentially. Owing to the great differences in these various forms of growth, occurring at the same time in this one layer of cells, portions may become so distorted that it

is often impossible to interpret or explain the cell arrangement. The rapidity with which these changes take place is apparent from the fact that in all the collections before July 6 and in most of the collections on that date (Fig. 9), no trace of cambium or periderm is to be found, but less than a week later, a large part of the surface of the fruit is found to include an active cork cambium and a well formed layer of cork (Fig. 12).

The first trace of cambium is found in a few cells on and after July 6. It appears as a thin radial wall in the inner cell of the epidermal layer (Fig. 10). The cambium cell is initiated always in a cell of epidermal origin and never



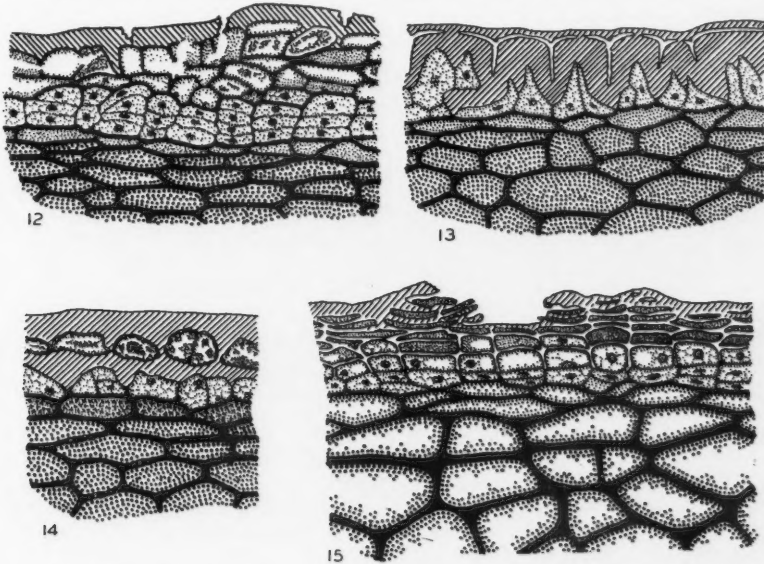
FIGS. 10-11. Radial sections through outer layer; cuticle singly cross-hatched. FIG. 10. July 6. Initiation of the cambium layer. Note that the division is in the innermost cell of epidermal origin, the tangential wall is very delicate or thin and the two resulting cells are typically meristematic in structure. $\times 320$. FIG. 11. July 9. A small patch of recently formed and active cambium. The contents of the outer epidermal cells have started to disintegrate. $\times 320$.

in a cell of sub-epidermal origin. This division of the inner epidermal cell by a radial wall very soon becomes quite common, so that, within a very few days, patches of such cells are found frequently throughout the layer (Fig. 11). These cells immediately start to divide rapidly by tangential walls. The cells given off towards the outside mature and form typical radial rows of cork cells. During this process the outer cells of the original epidermal layer die, their contents disintegrate and their walls rupture. Also the cuticle, by rupturing in many places, forms the first indication of the surface cracks so typical of a russet apple (Fig. 12).

From this stage on there is nothing in the development of the russet layer which is in any way different from the development of any typical periderm or cork. The cuticle remains on the outside, and immediately beneath it are the crushed epidermal cells and the crushed outer cork cells. The ruptures in the cuticle and crushed outer cells enlarge as the fruit enlarges, and form the network of minute cracks so characteristic of the ripe russet apple. These cracks are quite conspicuous in a cross section of the mature periderm (Fig. 15). During July and August, while the fruit is attaining its maximum size, the periderm becomes the dominant outer protective layer. By this time the cork cambium cells form an even tangential row which conforms very little to the unevenness and cracks on the outer surface. As the mature russet layer appears to be typical periderm, the structure of which is so well

known, and adequately described in so many textbooks, there is no need to give a detailed description here.

In the Golden Russet apple there are, of course, portions of the surface which do not become russeted. The structure of the protective layers in these regions is worthy of at least a brief description. In general, the epidermis of the non-russeted portions is either one or two cells thick. Where it is single celled, the cuticle is very thick and it is usually folded or convoluted



FIGS. 12-15. Radial sections through outer layer; cuticle singly cross-hatched. FIG. 12. July 9. A stage slightly more advanced than shown in Fig. 11. The cambium has extended further and in places it has already given off cells which will later become cork. The outer epidermal cells are crushed and ruptured, and the cuticle has cracked in various places. $\times 370$. FIG. 13. Aug. 6. A convoluted cuticle from a non-russeted portion. The epidermal cells have apparently not divided and hence the layer in such a region is chiefly one cell thick. $\times 370$. FIG. 14. Aug. 13. A typical two layered cuticle from a non-russeted portion. $\times 370$. FIG. 15. Sept. 24. Mature periderm or russet, including a cross-section of a typical "crack". $\times 370$.

(Fig. 13). Tetley (5, p. 166, and Fig. 9) reports a cuticle condition like this for the "Lord Suffield" variety. Where the epidermis is two cells thick, the cuticle is often in two distinct layers, with the outer halves of the epidermal cells forming a row of cells between the two layers of cuticle (Fig. 14). Zschokke (7) describes this condition and explains it by saying that the inner half of the epidermal cell assumes the usual function of the epidermis and continues to form cuticle, with the inevitable result that the outer half of the epidermal cell is pushed out. Tetley (6, p. 284, and Fig. 4, c) describes a somewhat similar cuticle structure for the "Bramley's Seedling" variety, and refers to the inner layer of cuticle as "Fatty deposits between the lower

tangential wall of the epidermal cells and the sub-epidermal cells” Whatever the correct description or explanation may be, a cuticle that has the appearance of being in two layers is quite typical of non-russeted portions of the Golden Russet apple.

When examining the protective layers of such an apple as the Golden Russet, it is well to bear in mind that the different structures described above are not always distinct and sharply differentiated from each other. The various types merge one with the other, forming a tissue which is often quite complex.

Conclusion

The net result of this study is that the finding of Zschokke is confirmed. That is, in the apple, normal russetting originates in the epidermis. However there are those, who, like the author, find it necessary to identify these structures, and to them the more detailed descriptions and figures given in the present article should be of considerable assistance.

Acknowledgments

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THE QUALITY AND GRADING OF FROSTED WHEAT

ANNUAL SURVEYS OF THE 1930 TO 1935 WESTERN CANADIAN CROPS¹

By J. G. MALLOCH², W. F. GEDDES³, R. K. LARMOUR⁴
AND A. G. MCCALLA⁵

Abstract

Fifteen officially graded samples of frosted wheat were collected from each of grades No. 3 Northern to No. 6, for 1930, 1931, 1932 and 1933, and 20 samples from each of these grades in 1934 and 1935. Physical classification of the kernels in each sample showed that the present system of grading is efficiently applied. While this system usually gives grades of frosted wheat, the averages of which fall in the right order with respect to combined milling and baking quality, it fails to give close indication of the baking quality, particularly of individual samples.

A statistical examination of the relation between quality characteristics and grading factors showed that milling quality is closely related to the percentages of immature and heavily frosted kernels and also to the weight per measured bushel. Baking quality is not closely related to any of the grading factors now in use. Protein content is the best single index of baking quality, and the relation is improved if the percentages of immature and heavily frosted kernels are taken into account. The quality decreases more or less uniformly over the entire protein range with increasing percentages of immature kernels, but the presence of heavily frosted kernels is related to greater quality decreases in low protein samples than in high protein samples. The correlation between yield of straight flour and loaf volume facilitates simultaneous evaluation of milling and baking quality in grading. The application of these findings to practical grading is discussed.

Introduction

In 1928, owing to limited rainfall following germination, which resulted in uneven growth, and to late heavy frosts, a large portion of the wheat crop contained many types of frost damage together with green and immature kernels. This provided an opportunity for studying the efficacy of the Canadian grain grading system as applied to such wheats and also for determining the relative effects of the various types of damage on milling and baking quality. It was found (5) that the grading system in use that year gave a correct indication of the average relative milling and baking quality of the various statutory and commercial grades, excepting No. 4, which was superior in baking strength to the higher grades.

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Contribution from the Department of Field Crops, University of Alberta, Edmonton; Grain Research Laboratory, Board of Grain Commissioners, Winnipeg; Department of Agricultural Chemistry, University of Manitoba, Winnipeg; and Department of Chemistry (supported by the Saskatchewan Agricultural Research Foundation), University of Saskatchewan, Saskatoon; with financial assistance from the National Research Council of Canada. Published as Paper No. 128 of the Associate Committee on Grain Research of the National Research Council and the Dominion Department of Agriculture.

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The percentages of bran frosted, heavily frosted, immature and green kernels taken individually were not closely related to either flour yield or baking strength, but collectively they were found to exert an appreciable influence. This implied that the total percentage of damage, or conversely the percentage of sound kernels present, would form the most logical basis for the grading of wheat into the commercial grades.

In 1930, amendments were made to the Canada Grain Act introducing changes in the percentage of hard vitreous kernels required in the first four grades and making No. 4 a statutory grade. Frosted wheat may be placed in grades 3 Northern, 4 Northern, No. 5, No. 6 or Feed. In either of the Northern grades it must conform to the statutory definitions* as given in the Canada Grain Act, and in practice it must be comparable with standard samples approved by the Western Committee on Grain Standards as being in accordance with these definitions. The standards for the commercial grades (No. 5, No. 6 and Feed) are set by this committee each year, taking into consideration the general character of the crop. In essence, the grading factors used in the application of these standards to frosted wheat are the weight per measured bushel and the proportion and nature of damaged kernels.

The changes in grading, coupled with the fact that in 1928 the frost occurred when the wheat was nearly mature and extended into areas which do not usually produce frosted wheat, rendered it advisable to conduct similar studies in subsequent years. The present paper deals with the results of surveys of the six crops grown in 1930 to 1935.

Material and Methods

The material for this investigation was supplied by the Western Grain Inspection Division and comprised approximately 15 officially graded samples of each of grades No. 3 Northern to No. 6 in 1930 to 1933 inclusive, and 20 samples of each of these grades in 1934 and 1935. The samples were cleaned,

*Statutory definitions.

Number and name of grade	Minimum weight per bushel in pounds	Variety of grain	Percentage by weight of hard vitreous kernels, %	Standard of quality
No. 3 Manitoba Northern	57	Red spring wheat of fair milling quality.	25	Reasonably well matured, reasonably free from damaged kernels.
No. 4 Manitoba Northern	57	Red spring wheat	—	Reasonably well matured, but excluded from preceding grades on account of frosted or otherwise damaged kernels.

NOTE: The purity specifications are omitted.

subdivided and forwarded to the cereal research laboratories of the Universities of Alberta and Saskatchewan, and to one laboratory in Winnipeg (1930-1932, University of Manitoba; after 1932, Dominion Grain Research Laboratory).

The following tests were made:

Weight per measured bushel. The procedure used was that previously described (5).

Protein content. Determined by the usual Kjeldahl-Gunning method.

Physical classification. A 50-gram sample was separated by hand-picking into the following classes:

- (a) Sound:—well matured kernels free from frost damage.
- (b) Bran frosted:—kernels showing wrinkling of the bran which did not extend into the crease.
- (c) Heavily frosted:—all kernels showing frost damage not included in (b).
- (d) Immature:—fully formed kernels having a dark color, usually referred to as "bronzy" or "pink" kernels.

In the previous study a separate class was used for "kernels having a decided green color, usually shrivelled." In the present surveys the percentage of such kernels was very small and they were included with the "immature" class.

Some of the samples were found to contain small quantities of broken kernels, foreign matter, etc. This material was discarded and the percentage by weight calculated on the basis of the other groups taken as 100.

There is, of course, a considerable element of judgment in making such a classification and different observers might reasonably arrive at slightly different proportions of the various classes. However, there was frequent rechecking and the results throughout may be regarded as consistent.

Milling test. The samples were experimentally milled in each of the collaborating laboratories, using the technique outlined previously (5), but only a straight flour was produced instead of two grades. In this method standard samples of feed flour and shorts are employed, extraction of the flour from the shorts and the reduction of the feed flour being continued until the residues match the respective standards. The straight grade flour included all the flour with the exception of the feed flour, the two comprising the total. The straight flour does not constitute a constant percentage of the total flour, as the quantity of the former depends partly on the extent to which the feed flour has to be reduced to match the arbitrary standard.

Baking tests. In accordance with the usual policy of the Associate Committee on Grain Research, several baking formulas, designed to reveal the baking characteristics under a range of conditions, were employed. The results of only three of these are reported in detail. The results of two blend tests are used at one point in the statistical examination, but the other four formulas give little additional information. They were used, however,

in the preliminary study of the results. The formulas reported are all based on the "simple" test, which is identical with the A.A.C.C. basic test (3), using mechanical mixing and low-form baking tins.

(a) *Bromate formula*—Simple formula with the addition of 0.001 gm. potassium bromate; employed for all years.

(b) *Malt-phosphate formula*—Simple formula with the addition of 0.3 gm. diastatic malt (approx. 250° Lintner) and 0.1 gm. $\text{NH}_4\text{H}_2\text{PO}_4$; employed for the 1930, 1931 and 1932 crop samples.

(c) *Malt-phosphate-bromate formula*—Combination of formulas (a) and (b); employed for the 1933, 1934 and 1935 crop samples.

(d) *Blend-bromate formula*—Formula (a), but each sample blended with 50% of English flour; employed for 1930, 1931 and 1932 crop samples.

(e) *Blend-malt-phosphate-bromate formula*—Formula (c), but each sample blended with 50% of English flour; employed for 1933 and 1934 crop samples.

Physical Characteristics of the Grades

The mean values for weight per bushel and classes of kernels, arranged according to crop year and grade, together with the standard deviations of single samples, are given in Table I. The standard deviations show that there is a considerable spread in the values which enter into any of the means but that there is no evident trend in the magnitude of this variability with decreasing grade. As the variability affects the reliance that can be placed on the differences between the mean values, the statistical significance of these differences must be estimated before conclusions can be drawn.

When the standard deviation varies from grade to grade the analysis of variance is not strictly applicable since the z distribution will not be realized. Consequently F values (11) are shown only for these cases where the standard deviation is relatively constant. For the others an indication of the significance of the differences can be obtained by comparing them with the standard errors of the means obtained by dividing the standard deviations of single samples given in the table by the square root of the number of samples. Where a definite trend exists, additional reliance may be placed on the reality of the differences.

In general there is a definite lowering of weight per bushel and percentage of sound kernels, and corresponding increases in the percentages of the different forms of damage, from the higher to the lower grades. However, there are exceptions to this general rule. In 1931 grades, No. 5 and No. 6 do not show the expected relation. The differences in weight per bushel and percentage of bran-frosted and immature kernels are not significant. No. 6 has a higher mean value for sound kernels and a lower one for heavily frosted kernels than No. 5, but these differences also may not be significant. These are the only two grades which show a complete departure from the normal relation. Under the system of grading on the basis of weight per

TABLE I
WEIGHT PER BUSHEL AND CLASSES OF KERNELS

Grade†	No. of samples	Weight per bushel		Sound (1)		Bran frost (2)		Heavy frost (3)		Immature (4)	
		Mean, lb.	S.D., lb.	Mean, %	S.D., %	Mean, %	S.D., %	Mean, %	S.D., %	Mean, %	S.D., %
1930											
3°	15	63.8	1.3	63.9	17.1	16.3	16.2	18.3	6.6	1.7	1.0
4°	15	63.7	0.8	43.3	13.8	13.2	6.8	41.9	9.8	1.6	0.6
No. 5	15	62.2	1.5	20.9	10.9	22.2	9.4	51.8	13.0	5.1	3.3
No. 6	14	60.0	1.6	6.9	6.2	33.2	9.5	45.7	17.1	14.3	9.5
	F*	24.13		—		—		—		—	
1931											
3°	15	64.9	1.3	66.4	14.5	7.3	4.2	21.6	11.5	4.7	2.9
4°	15	63.6	1.1	38.2	20.9	10.5	6.2	46.6	19.2	4.8	3.4
No. 5	15	61.6	1.3	19.6	12.8	16.6	12.9	55.1	26.9	8.7	7.1
No. 6	15	61.5	1.8	24.1	14.1	16.0	14.4	50.9	20.2	9.1	7.7
	F*	19.46		24.70		—		7.72		1.92	
1932											
3°	15	64.2	1.4	56.1	12.6	19.4	9.9	23.5	9.5	1.0	0.6
4°	15	63.6	1.2	36.8	12.2	20.3	5.8	40.3	15.6	2.5	2.6
No. 5	15	62.8	1.2	22.2	14.6	19.5	7.2	53.7	20.2	4.6	2.6
No. 6	15	61.5	1.3	7.8	6.3	12.1	6.3	74.7	14.6	5.4	3.8
	F*	11.03		42.75		2.53		27.54		—	
1933											
3°	15	64.2	1.3	70.2	11.4	9.7	5.2	3.9	2.4	4.3	2.3
4°	15	63.5	1.4	49.8	9.8	18.5	10.2	13.6	8.8	7.7	3.8
No. 5	15	63.2	1.5	31.0	13.5	32.2	13.6	19.7	10.3	10.4	5.2
No. 6	15	61.9	1.6	14.2	8.0	29.2	9.5	36.2	17.1	19.6	10.4
	F*	6.78		74.08		18.86		—		—	
1934											
3°	20	64.6	1.2	74.2	6.3	13.0	6.8	1.4	1.0	9.1	6.6
4°	20	63.7	0.9	59.9	9.8	24.3	8.9	4.0	3.2	10.1	4.5
No. 5	20	59.1	1.1	32.9	13.9	32.9	10.7	6.7	7.5	26.0	16.7
No. 6	20	60.8	2.1	12.7	6.9	36.3	14.8	9.5	14.6	41.1	16.4
	F**	28.02		161.52		18.81		—		—	
1935											
3°	20	64.1	2.1	72.5	12.6	14.9	8.4	1.0	0.9	9.2	7.4
4°	20	63.1	2.3	52.0	13.0	25.7	11.4	2.1	1.9	17.4	14.2
No. 5	20	62.2	1.8	32.1	11.6	40.1	17.0	4.6	4.6	22.2	14.0
No. 6	20	59.8	2.1	19.7	9.4	44.8	16.4	5.6	7.0	44.8	18.2
	F**	15.92		77.78		11.27		—		23.66	

* Value of F at 5% point = 2.77.

** Value of F at 5% point = 2.71.

† 3°, 4° = 3 Northern, 4 Northern (Statutory grades).

No. 5, No. 6 (Commercial grades).

bushel and the appearance of the sample, it is inevitable that isolated anomalies in the relative percentages of individual classes of kernels will arise. The grain inspector must balance one form of damage against another. For example, the decreases in the percentage of bran frost from 3 Northern to 4 Northern in 1930, from 4 Northern to No. 6 in 1932, and from No. 5 to No. 6 in 1933, are balanced in each case by increases in the percentage of heavily frosted kernels; the increase in test weight from No. 5 to No. 6 in 1934 is balanced by a marked increase in the percentage of immature kernels; and the decrease in heavily frosted kernels from No. 5 to No. 6 in 1930 is balanced by increases in the percentages of immature and bran frosted kernels and a decrease in the test weight.

On the average the characteristics of the various grades conform closely to those to be expected from an efficient application of the present grading system.

Grade as an Index of Quality

If the grading system is satisfactory the combined milling and baking quality should decrease regularly without overlapping, from the higher to the lower grades. The grade averages for both milling yield and baking value should decrease, but in individual samples high milling yield may compensate for low baking quality, and *vice versa*. Variability in the character of the samples entering any grade would be expected even under an ideal system. Accordingly it is essential that in any discussion of the grading of wheat both milling quality and baking quality should be taken into account.

MILLING QUALITY

Table II shows the mean yields of straight and total flour with their standard deviations and the yield of straight flour expressed as a percentage of the total flour. The standard deviations are reasonably constant for any one year and the analysis of variance can be applied to determine the significance of the differences between the means. The *F* values obtained are in all cases highly significant.

In all years there is a downward trend in yield of straight and total flour as the grade passes from 3 Northern to No. 6. Furthermore, there is a decrease in the percentage of total flour obtained as straight flour. This implies that in commercial practice a greater proportion of the flour from the lower grades of wheat would have to be excluded from the top patents in order to obtain flours approximating in color and ash content those obtained from the higher grades of wheat.

The grade thus gives a reasonably satisfactory indication of the probable milling quality of bulk lots of frosted wheat, though not a clear-cut classification of the individual samples with respect to this character.

BAKING QUALITY

In assessing the baking quality from the results of the baking tests, the loaf volume must be given first consideration, as it gives a direct indication of those qualities desired in Canadian wheat for blending with other wheats

TABLE II
FLOUR YIELD

Grade	No. of samples	Total flour yield		Str. grade flour yield		Str. grade flour as % total
		Mean, %	S.D., %	Mean, %	S.D., %	Mean, %
1930 Crop						
3°	15	72.1	1.7	65.5	0.5	92.3
4°	15	71.7	1.0	64.3	0.9	91.1
No. 5	15	68.5	1.4	62.2	1.8	89.0
No. 6	14	66.0	2.5	60.2	1.1	87.0
	F*	38.9		68.4		
1931 Crop						
3°	15	71.0	1.2	64.7	1.1	91.0
4°	15	70.2	1.2	63.5	1.4	90.4
No. 5	15	67.9	2.5	61.6	2.7	89.9
No. 6	15	67.4	1.9	60.3	2.1	89.4
	F*	12.45		14.29		
1932 Crop						
3°	15	73.0	2.6	66.8	2.9	91.0
4°	15	71.4	1.7	64.9	2.0	90.7
No. 5	15	69.6	1.7	61.9	2.4	88.8
No. 6	15	67.0	2.9	57.8	4.1	86.1
	F*	17.36		24.32		
1933 Crop						
3° ;	15	73.2	0.9	68.8	1.0	94.0
4° ;	15	72.5	1.5	67.4	1.5	93.3
No. 5	15	71.9	1.8	66.5	1.9	92.8
No. 6	15	69.6	1.4	63.8	1.5	92.0
	F*	17.67		28.02		
1934 Crop						
3°	20	73.2	0.9	69.1	0.8	94.5
4°	20	72.1	1.1	67.6	1.2	93.8
No. 5	20	70.1	2.0	65.0	2.7	92.6
No. 6	20	67.4	1.9	60.9	2.4	90.3
	F†	52.82		8.60		
1935 Crop						
3°	20	73.2	1.9	68.4	1.7	93.5
4°	20	72.0	2.0	66.7	2.0	92.6
No. 5	20	70.5	2.0	64.6	2.2	91.7
No. 6	20	65.6	1.6	58.7	1.8	89.4
	F†	62.45		97.15		

* Value of F at 5% point = 2.77.

† Value of F at 5% point = 2.71.

by millers overseas. With sound wheat a high volume is generally associated with good absorption, and with good texture and appearance of the loaf. In frosted wheat this may not hold and it is necessary to take full account of the other loaf characteristics, since dough quality is often reflected in these.

The mean results of the baking tests with the standard deviations of single samples are given in Table III. There is a great variation of the standard deviations from grade to grade with, in most cases, no apparent trend. Criteria for judging the significance of the differences in Table III can be established in the same manner as for Table I (see page 570). As several characters must be taken into account and as the results are not consistent from year to year, it seems desirable to discuss each year's results separately before arriving at a general conclusion.

1930 Crop

There was practically no difference between grades 3 and 4 Northern. No. 5 was similar to these two grades in volume-producing power, but decidedly below them in general quality, because of the poorer texture and crumb color of the loaves. The absorption was practically the same for grades 3 and 4 Northern, and increased in No. 5 and No. 6. Normally, increased absorption adds to the value of a sample. There is some doubt, however, that increased absorption in the lower grades is as commercially valuable as it is in the higher grades. While greater water-absorbing capacity, regarded as an isolated character, is undoubtedly desirable, in frozen wheat it is generally indicative of undesirable modification of the dough characters and must be taken as an index of the severity of frost damage. We must conclude, therefore, that the average baking quality of the grades was the same for 3 Northern and 4 Northern, slightly inferior in No. 5 and decidedly inferior in No. 6. It follows from this and from the extent of the variability within grades that the grade of the individual samples was not a good index of their baking quality.

1931 Crop

In this year the grade was a very poor index of baking quality of the samples tested. No. 6 had a higher loaf volume than 3 Northern and the loaf characters of the two grades were almost identical. No. 6 had a higher absorption, but this was the only indication that the quality of this grade might have been affected by frost. No. 5 had a higher loaf volume than No. 4, and was slightly better in most loaf characters, with little difference in absorption. Both these grades were inferior to 3 Northern and No. 6. Since the averages of the grades did not fall in the proper order the placing of many of the individual samples for baking quality must have been faulty.

1932 Crop

Grades 3 and 4 Northern were almost identical in baking quality. The results for all the characters placed No. 5 well below 4 Northern, and No. 6 decidedly lower still. Variability increased quite regularly with lowering of

TABLE III
BAKING QUALITY

Grade	No. of samples	Absorption (13.5% M.B.)		General appearance		Crumb color		Crumb texture		Loaf volume	
		Mean, %	S.D., %	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean, cc.	S.D., cc.
1930											
<i>Bromate formula</i>											
3°	15	65.0	0.9	8.5	0.7	7.5	0.2	7.6	0.3	635	45.2
4°	15	65.5	0.8	8.6	0.6	7.3	0.6	7.5	0.5	612	35.7
No. 5	15	67.9	1.3	8.6	1.2	5.8	1.3	6.3	1.6	607	82.6
No. 6	14	71.1	1.2	7.8	1.0	4.7	1.0	5.0	1.2	545	76.4
	<i>F*</i>	94.47		2.61		—		—		4.99	
<i>Malt-phosphate formula</i>											
3°	15	62.8	0.9	9.1	0.5	7.4	0.5	6.9	0.8	658	36.6
4°	15	62.9	1.3	9.0	0.4	6.8	0.8	7.0	0.7	658	29.7
No. 5	15	64.7	1.5	8.6	0.8	4.7	1.3	5.1	1.7	624	79.2
No. 6	14	67.6	1.6	8.0	0.9	3.2	1.1	3.6	1.0	602	74.0
	<i>F*</i>	39.36		7.52		53.73		27.48		2.96	
1931											
<i>Bromate formula</i>											
3°	15	65.2	0.9	8.7	0.8	7.0	0.9	7.2	0.6	640	108.4
4°	15	65.2	1.0	8.5	0.8	6.2	0.7	6.6	0.8	555	61.7
No. 5	15	65.7	0.7	8.6	0.8	6.4	1.1	6.8	1.1	590	86.6
No. 6	15	67.3	0.8	9.0	0.8	6.9	1.0	7.1	0.6	680	93.2
	<i>F*</i>	19.26		0.99		2.41		1.86		5.36	
<i>Malt-phosphate formula</i>											
3°	15	63.1	2.3	8.8	0.7	7.0	0.9	7.3	0.5	500	78.1
4°	15	62.9	2.3	8.3	0.6	6.1	0.7	6.8	0.5	534	52.0
No. 5	15	64.6	1.2	8.3	0.6	6.2	0.9	6.7	0.5	580	60.9
No. 6	15	66.5	1.1	8.7	0.5	6.6	0.6	6.8	0.4	640	66.4
	<i>F*</i>	11.98		2.71		3.63		4.26		3.36	
1932											
<i>Bromate formula</i>											
3°	15	68.1	0.6	9.5	0.3	6.8	0.4	7.3	0.3	739	69.7
4°	15	68.0	0.5	9.2	0.7	6.4	0.7	7.0	0.5	728	82.5
No. 5	15	69.8	1.8	8.5	1.2	5.4	1.0	5.9	1.3	616	109.8
No. 6	15	73.9	1.5	7.8	1.1	4.3	1.1	4.5	1.3	578	148.6
	<i>F*</i>	69.05		—		23.28		—		7.92	
<i>Malt-phosphate formula</i>											
3°	15	69.5	1.2	8.7	0.4	6.5	0.4	6.9	0.3	727	31.8
4°	15	68.9	1.0	9.0	0.5	6.8	0.5	7.1	0.4	748	78.4
No. 5	15	71.8	2.8	8.2	0.9	5.8	0.8	6.0	0.7	624	93.0
No. 6	15	77.4	2.3	7.7	0.8	4.9	1.0	5.7	0.7	571	128.5
	<i>F*</i>	37.68		11.46		10.97		21.57		—	

TABLE III—*Concluded*
BAKING QUALITY—*Concluded*

Grade	No. of samples	Absorption (13.5% M.B.)		General appearance		Crumb color		Crumb texture		Loaf volume	
		Mean. %	S.D., %	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean, cc.	S.D., cc.
1933											
Bromate formula											
3°	15	65.6	1.1	8.9	1.0	5.8	1.2	6.4	1.6	629	81.9
4°	15	65.6	0.9	8.4	1.1	5.2	1.6	5.6	2.1	600	109.6
No. 5	15	66.4	1.2	7.9	1.5	3.8	1.6	4.4	2.0	529	69.4
No. 6	15	68.2	1.3	6.6	1.9	2.4	1.5	3.0	1.7	472	84.8
	F*	15.41		6.66		14.51		9.16		91.40	
Malt-phosphate-bromate formula											
3°	15	62.1	0.8	7.8	0.6	6.0	1.2	6.4	1.2	679	98.3
4°	15	62.3	0.7	7.5	0.9	5.4	1.6	5.6	1.4	648	120.4
No. 5	15	62.9	0.8	7.4	0.9	4.3	1.2	4.7	1.2	563	70.0
No. 6	15	63.7	0.7	6.2	1.3	2.9	1.4	3.2	1.2	488	84.1
	F*	13.62		7.30		14.09		15.93		114.82	
1934											
Bromate formula											
3°	20	64.5	0.8	3.5	1.0	5.3	1.9	5.5	2.1	592	114.5
4°	20	64.6	0.7	3.5	1.1	5.5	2.2	5.5	2.4	601	118.0
No. 5	20	65.4	1.5	3.0	1.7	4.5	2.5	4.5	2.7	515	133.8
No. 6	20	67.1	1.8	2.5	1.7	2.5	2.2	3.0	2.2	444	100.1
	F†	17.51		2.07		7.95		6.54		7.89	
Malt-phosphate-bromate formula											
3°	20	61.7	0.8	3.5	1.0	5.0	2.0	5.0	2.0	714	159.9
4°	20	62.3	0.7	3.5	1.3	5.5	2.2	5.5	2.3	731	179.4
No. 5	20	63.7	1.5	2.5	1.6	4.0	2.2	4.0	2.4	591	173.3
No. 6	20	65.7	1.5	1.5	1.2	1.5	1.2	2.0	1.6	468	115.7
	F†	45.31		8.45		14.81		12.33		11.88	
1935											
Bromate formula											
3°	20	67.6	0.9	4.0	0.3	7.0	0.9	7.5	1.0	693	88.2
4°	20	68.0	0.9	4.0	0.7	6.0	1.3	6.5	1.6	603	104.7
No. 5	20	69.6	1.1	4.0	1.1	5.0	1.8	5.5	1.0	588	98.2
No. 6	20	72.3	1.0	2.0	0.8	2.0	0.9	2.0	0.9	431	61.1
	F†	93.61		36.77		62.60		51.79		29.50	
Malt-phosphate-bromate formula											
3°	20	64.7	0.7	4.0	0.4	6.0	0.9	6.5	0.8	757	101.3
4°	20	65.4	0.7	4.0	0.7	5.0	1.2	5.5	1.5	670	117.4
No. 5	20	67.0	0.9	3.5	1.0	4.5	1.6	4.5	1.7	630	106.3
No. 6	20	69.3	0.7	2.0	0.6	1.5	0.7	1.5	0.8	463	74.6
	F†	152.31		30.18		56.54		123.40		29.88	

* Value of *F* at 5% point = 2.77.† Value of *F* at 5% point = 2.71.

the grade, beginning reasonably low in the Northern grades. The grading failed to differentiate the baking quality of the more lightly frosted grain, but was satisfactory for that more heavily frosted.

1933 Crop

The means show the baking quality to decrease with the grade. The variability in loaf volume was quite high in 4 Northern, and some of the individual samples in this grade undoubtedly had baking quality which should have put them either in 3 Northern or No. 5.

1934 Crop

The results for the average quality were similar to those for 1932. Grades 3 and 4 Northern were almost identical in baking quality. The relatively high variability in all grades for volume, texture and color indicate that the grade was not a good index of the baking quality of individual samples.

1935 Crop

This year was similar to 1933. On the average the grade was a good index of baking quality. The high standard deviations of the first three grades, and particularly of 4 Northern, show that some of the individual samples were wrongly placed.

1930-1935

In two of the six years the grading gave a good indication of the average baking quality. In three years the two higher grades were not properly differentiated but they had better quality than the other two grades, the latter standing in the correct relation to each other. In one year (1931) the grading system failed to give any proper classification with respect to baking quality, and in all years the grade was unreliable as an index of the baking quality of individual samples.

COMBINED MILLING AND BAKING QUALITY

To ascertain the correctness of the grading it is necessary to arrive at a judgment of the combined milling and baking value of the different grades. Obviously if both flour yield and baking quality decrease, or if one of these stays constant and the other decreases, there can be no doubt that the value decreases. Where these two factors vary in the opposite sense, the comparison between the samples will depend on the relative importance attached to yield and to quality in view of the purpose for which the wheat is to be used.

Since Canadian wheat is used under a wide variety of conditions, it is not possible to assign values which will be applicable in all cases. No mathematical relation between the different quality characteristics has ever been established and a definite numerical index of value cannot be calculated. However, by studying the ranking of the grades for milling quality and baking quality separately it is possible to form an opinion of the combined value. To express our opinion in summary form, we have assigned alphabetical values (Table IV) to the grades, using A for 3 Northern and con-

tinuing through the alphabet for progressively decreasing values. The scale was designed so that, if the grading system gave values which decreased with uniform spreads, the placings for grades 3 Northern to No. 6 would be A, D, G, J. The letters intermediate between these are used to indicate intermediate values. Thus, if 4 Northern has a value of B it is considered to be only slightly poorer than 3 Northern.

TABLE IV
APPROXIMATE RELATION OF THE COMBINED MILLING AND BAKING VALUES OF THE GRADES

Grade	Ideal	1930	1931	1932	1933	1934	1935
3°	A	A	A	A	A	A	A
4°	D	B	C	B	C	B	D
No. 5	G	D	C	E	F	F	E
No. 6	J	F	B	J	I	J	J

In every year but 1931 there was a progressive decrease in quality with lowering of grade. In 1933 and 1935 the relation was good throughout; in 1932 and 1934 the spread between 3 and 4 Northern was small, but otherwise the grading was good. In 1930 the spread over the four grades was narrow, but the grades were differentiated nevertheless. It appears that, in most years, the present grading system will classify frosted wheat so that the average quality of the grades will fall in descending order, but not with uniform spreads. In bulk lots the grade is a fairly good index of milling quality but a relatively poor index of baking quality, and with individual samples the indication is less reliable.

Relation between Grading Factors and Quality Characteristics

Any improvement in the grading of frosted wheat must come through more accurate evaluation of the quality of individual samples, since this would bring about a better relation between grades and a reduction in the variability within grades. To find out whether such improvement is possible, it is necessary to ascertain whether the present grading factors are being used to the best advantage and whether there are any additional factors that should be taken into consideration. This can be done by statistical examination of the relation between the various factors and the quality characteristics, over all four grades.*

MILLING QUALITY

In general the simple correlations between percentage of sound or immature kernels or weight per bushel, and straight or total flour yield (Table V) are statistically significant, and while the coefficients are not high enough to permit certain prediction of flour yield, the utility of these factors for grading is apparent. There is little practical difference in the closeness of association

* Readers who prefer to skip the highly statistical argument of the following sections will find the conclusions summarized under the heading "Discussion" on page 589.

for these three factors, and if a single factor were to be used as an index of milling yield the choice would have to be made on the character of the relations as shown by the regression coefficients. However, the multiple correlations between straight and total flour yield, and bran frosted, heavily frosted, and immature kernels show that a more accurate estimate of the yielding capacity of the samples can be obtained if more factors are taken into account. Moreover, since these multiple correlations are higher than any of the simple correlations, it seems preferable to consider the different forms of damage separately rather than to grade on the basis of the total percentage of damage or conversely, on the percentage of sound kernels.

TABLE V
RELATION BETWEEN FLOUR YIELD AND PHYSICAL CHARACTERISTICS OF WHEAT

			Simple correlation coefficients					Simple correlation coefficients	
			Straight flour yield, (s)	Total flour yield, (t)				Straight flour yield, (s)	Total flour yield, (t)
1930 Crop*					1931 Crop*				
Sound	(1)		.79	.75	Sound	(1)		.46	.41
Bran frost	(2)		-.61	-.71	Bran frost	(2)		-.38	-.49
Heavy frost	(3)		-.35	-.19	Heavy frost	(3)		-.15	-.03
Immature	(4)		-.78	-.84	Immature	(4)		-.50	-.60
Weight per bushel (w)			.78	.84	Weight per bushel (w)			.63	.65
Multiple correlation coefficients					Multiple correlation coefficients				
$R_{s.234} = .86$			} 5% pt. = .36		$R_{s.234} = .67$			} 5% pt. = .36	
$R_{t.234} = .92$					$R_{t.234} = .72$				
1932 Crop*					1933 Crop*				
Sound	(1)		.68	.59	Sound	(1)		.76	.58
Bran frost	(2)		.10	-.03	Bran frost	(2)		-.42	-.32
Heavy frost	(3)		-.56	-.41	Heavy frost	(3)		-.58	-.49
Immature	(4)		-.62	-.72	Immature	(4)		-.70	-.70
Weight per bushel (w)			.60	.57	Weight per bushel (w)			.67	.61
Multiple correlation coefficients					Multiple correlation coefficients				
$R_{s.234} = .81$			} 5% pt. = .36		$R_{s.234} = .83$			} 5% pt. = .36	
$R_{t.234} = .82$					$R_{t.234} = .76$				
1934 Crop†					1935 Crop†				
Sound	(1)		.51	.85	Sound	(1)		.79	.75
Bran frost	(2)		-.28	-.42	Bran frost	(2)		-.12	-.04
Heavy frost	(3)		-.14	-.21	Heavy frost	(3)		-.46	-.35
Immature	(4)		-.47	-.82	Immature	(4)		-.78	-.80
Weight per bushel (w)			.40	.70	Weight per bushel (w)			.81	.86
Multiple correlation coefficients					Multiple correlation coefficients				
$R_{s.234} = .53$			} 5% pt. = .22		$R_{s.234} = .90$			} 5% pt. = .22	
$R_{t.234} = .89$					$R_{t.234} = .87$				

* Value of r at 5% point = .26.

† Value of r at 5% point = .22.

The partial regression coefficients describing the relation of flour yield to damage are given in Table VI. As those for bran frost are low and uniformly insignificant, this class of kernels can give no useful indication of yield. The

TABLE VI
RELATION OF STRAIGHT AND TOTAL FLOUR YIELD TO PERCENTAGES OF DAMAGED KERNELS

Year	Partial regression coefficient, % per 1%			Significance, <i>t</i> value (5% point = 1.96)		
<i>Straight flour yield</i>						
	$b_{s\ 2-24}$	$b_{s\ 3-24}$	$b_{s\ 4-23}$	$b_{s\ 2-24}$	$b_{s\ 3-24}$	$b_{s\ 4-23}$
1930	-.07	-.09	-.40	0.99	2.22	3.14
1931	-.04	-.05	-.27	1.05	2.49	3.12
1932	-.07	-.11	-.70	0.68	2.86	2.79
1933	-.03	-.06	-.16	0.90	2.31	2.93
1934	-.08	-.10	-.16	1.32	1.07	3.41
1935	-.07	-.19	-.18	1.54	1.25	5.11
<i>Total flour yield</i>						
	$b_{t\ 2-24}$	$b_{t\ 3-24}$	$b_{t\ 4-23}$	$b_{t\ 2-24}$	$b_{t\ 3-24}$	$b_{t\ 4-23}$
1930	-.06	-.10	-.32	1.15	2.94	3.13
1931	-.06	-.03	-.24	1.48	1.92	3.13
1932	-.06	-.06	-.66	0.90	2.21	3.66
1933	-.01	-.04	-.14	0.34	1.92	3.30
1934	-.05	-.07	-.12	1.56	1.38	5.08
1935	-.04	-.16	-.15	1.12	1.26	5.16

s = straight flour yield. *t* = total flour yield. 2 = bran frost. 3 = heavy frost. 4 = immature.

relation of heavy frost is more definite, particularly with straight flour yield, and the coefficients for immature kernels are significant throughout. The differences between the regression coefficients in a single year are insignificant in two-thirds of the comparisons, but on the average of the six years they are significant. The greatest decrease in flour yield for a unit increase in damage is obtained with immature kernels, followed by heavy frost, while the effect of bran frost is negligible.

The weight per measured bushel is related to the percentage of damage in the samples (Table VII). The association is closest with immature kernels and, with the exception of 1930, negligible or statistically insignificant with bran frost. The regression coefficients show too that the effect of the different forms of damage on weight per bushel is very similar in general character to their effect on flour yield. This similarity is particularly valuable as it relates two separately determined indices of flour yield.

It has been pointed out that the present grading gives a fair indication of flour yield, and the utility of the weight per bushel can be judged from a covariance analysis of weight per bushel and flour yield (Table VIII). The

TABLE VII
RELATION OF WEIGHT PER BUSHEL TO PERCENTAGE OF DAMAGED KERNELS

Year	Bran frost (2)	Heavy frost (3)	Immature (4)	Significance		
Simple correlation coefficients				Value of <i>r</i> at 5% point		
	<i>r_{w2}</i>	<i>r_{w3}</i>	<i>r_{w4}</i>			
1930	-.64	-.19	-.84	.26		
1931	-.28	-.37	-.49	.26		
1932	-.05	-.53	-.44	.26		
1933	-.23	-.60	-.36	.26		
1934	-.26	-.41	-.62	.22		
1935	-.05	-.36	-.74	.22		
Partial regression coefficient, lb. per 1%				<i>t</i> value (5% point = 1.96)		
	<i>b_{w2-34}</i>	<i>b_{w3-24}</i>	<i>b_{w4-23}</i>	<i>b_{w2-34}</i>	<i>b_{w3-24}</i>	<i>b_{w4-23}</i>
1930	-.03	-.03	-.21	0.99	1.32	3.38
1931	-.01	-.06	-.27	0.29	3.75	3.75
1932	-.07	-.05	-.16	1.97	3.53	1.84
1933	-.01	-.06	-.04	0.35	3.30	1.69
1934	-.01	-.10	-.07	0.47	2.99	4.29
1935	-.01	-.16	-.10	0.29	1.74	4.65

TABLE VIII
RELATION OF WEIGHT PER BUSHEL AND FLOUR YIELD WITHIN AND BETWEEN GRADES

Year	Simple correlation coefficients								
	Straight flour yield (<i>s</i>)			Total flour yield (<i>t</i>)			5% point		
	<i>r_{ss}</i>			<i>r_{tt}</i>					
	Total all grades	Between grades	Within grades	Total all grades	Between grades	Within grades	Total all grades	Between grades	Within grades
1930	.78	.97	.43	.84	.98	.63	.26	.95	.26
1931	.63	.99	.33	.65	.97	.39	.26	.95	.26
1932	.60	1.00	.27	.57	1.00	.26	.26	.95	.26
1933	.67	1.00	.50	.61	.99	.42	.26	.95	.26
1934	.40	.99	.07	.70	.99	.28	.22	.95	.22
1935	.81	1.00	.71	.86	1.00	.80	.22	.95	.22

significant correlations between grades show satisfactory differentiation, but the significance of most of the "within grades" correlations indicates that it is possible to reduce the variability through stricter limits for test weight.

Milling quality cannot be judged solely by flour yield. The ease with which the flour can be separated from the bran is also an important aspect of quality. Some measure of this can be obtained from the relative yields of "total" and straight flour. If the simple correlations (Table V) between the two types of flour and the percentage of heavily frosted and immature

kernels are compared, we find that, on the whole, immaturity is more closely associated with total flour yield than with straight flour yield, while the reverse is true for the percentage of heavily frosted kernels. It is probable that immaturity is related primarily to the proportion of bran while the percentage of heavily frosted kernels is more closely related to the ease of separation.

BAKING QUALITY

Although loaf volume is not the sole measure of the complicated and inter-related group of characteristics known collectively as baking quality, it is a good index of "strength" which is so desirable in Canadian wheat. Therefore, the utility of grading factors can be best studied by examining their relation to loaf volume.

The simple correlations (Table IX) of the various classes of kernels with loaf volume are all low and in the first two years of the survey many of them are statistically insignificant. Even the best relation, that with the percentage of sound kernels, is too low to provide a reliable basis for grading with respect to baking quality. The multiple correlations showing the combined relation of bran and heavy frost and immature kernels to loaf volume are slightly higher than the correlations obtained with the sound kernels. Thus grading taking into account the individual kinds of damage might be slightly better

TABLE IX
RELATION BETWEEN LOAF VOLUME AND CLASSES OF KERNELS

Year	Simple correlation coefficients					Multiple correlation coefficients	
	Sound (1)	Bran frost (2)	Heavy frost (3)	Immature (4)	5% point	$R_{.234}$	5% point
<i>Bromate formula</i>							
1930	.40	-.36	-.11	-.47	.26	.51	.36
1931	.17	.14	-.30	.28	.26	.35	.36
1932	.63	.32	-.64	-.35	.26	.70	.36
1933	.47	-.49	-.48	-.31	.26	—	—
1934	.53	-.38	-.26	-.40	.22	—	—
1935	.60	-.31	-.32	-.42	.22	—	—
<i>Malt phosphate formula</i>							
1930	.36	-.40	-.03	-.43	.26	—	—
1931	.06	.12	-.19	.26	.26	—	—
1932	.60	.24	-.58	-.36	.26	—	—
<i>Malt phosphate bromate formula</i>							
1933	.53	-.50	-.49	-.41	.26	.67	.36
1934	.58	-.40	-.28	-.44	.22	.60	.31
1935	.61	-.36	-.32	-.41	.22	.65	.31

than grading on the basis of the percentage of sound kernels alone, provided the partial regressions of loaf volume on percentage of kernels were known in advance for each class of kernel, a condition not realizable in practice. In any event, the comparatively low values of the multiple correlations indicate that other factors affecting loaf volume have been left out of consideration.

It was shown (5) that the percentage of protein had an important effect on the baking quality of frosted wheat of the 1928 crop. It is well established that the major factor affecting the capacity of sound Canadian hard red spring wheat to produce loaf volume is the protein content. Immaturity and frost, by deteriorating protein quality, may diminish this relation but need not destroy it.

The soundness of this view is demonstrated by the results of an analysis of the covariance of loaf volume and protein content (Table X). The simple correlations for all grades are, on the whole, higher than the multiple cor-

TABLE X
RELATION OF WHEAT PROTEIN AND LOAF VOLUME WITHIN AND BETWEEN GRADES

Year	Simple correlation coefficients			5% point		
	Total all grades	Between grades	Within grades	Total all grades	Between grades	Within grades
<i>Bromate formula r6b</i>						
1930	.75	.57	.80	.26	.95	.26
1931	.83	.90	.80	.26	.95	.26
1932	.83	.83	.97	.26	.95	.26
1933	.78	.96	.76	.26	.95	.26
1934	.89	.89	.91	.22	.95	.22
1935	.62	.74	.74	.22	.95	.22
<i>Malt-phosphate formula r6c</i>						
1930	.65	.20	.67	.26	.95	.26
1931	.68	.94	.58	.26	.95	.26
1932	.69	.44	.63	.26	.95	.26
<i>Malt-phosphate-bromate formula r6d</i>						
1933	.81	.97	.80	.26	.95	.26
1934	.88	.89	.92	.22	.95	.22
1935	.62	.68	.75	.22	.95	.22

relations involving the three classes of damage (Table IX) or, in other words, the protein content gives a better indication of baking quality than the factors now used in grading. However, the relation is by no means perfect. The fact that the "between grades" simple correlation coefficients are not significant, and that the "within grades" correlations tend to be higher than the correlations over all grades, indicates that the relation between protein and loaf volume is affected by the proportion of damage in the sample, and that the relation can be improved if this is taken into account.

TABLE XI

RELATION BETWEEN LOAF VOLUME, AND FORMS OF DAMAGE AND PROTEIN (MULTIPLE CORRELATION)

Year	Multiple correlation coefficients		
	Bromate formula $R_b .2346$	Malt-phosphate-bromate formula $R_d .2346$	5% point
1930	.90	—	.40
1931	.85	—	.40
1932	.92	—	.40
1933	.86	.90	.40
1934	.99	.99	.33
1935	.77	.83	.33

2 = bran frost. 3 = heavy frost. 4 = immature.
6 = wheat protein.

TABLE XII

RELATION BETWEEN LOAF VOLUME, AND DAMAGED KERNELS AND PROTEIN CONTENT (PARTIAL REGRESSIONS)

Year	Partial regression coefficient, cc. per 1%			
	$b_v 2-346$	$b_v 3-246$	$b_v 4-236$	$b_v 6-234$

Bromate formula

1930	-0.6	0.1	-4.1	60.6
1931	-3.9	-0.6	14.2	93.6
1932	0.4	-1.8	-3.4	63.3
1933	-1.2	-2.4	-0.7	52.8
1934	-1.9	-12.7	1.3	70.7
1935	-3.2	-1.2	-3.4	52.8

Malt-phosphate formula

1930	-1.0	0.2	-2.7	47.0
1931	-1.5	-0.3	7.1	37.2
1932	-0.4	-1.8	-5.0	43.5

Malt-phosphate-bromate formula

1933	-1.0	-2.3	-2.3	61.8
1934	-3.7	-6.6	-1.7	85.1
1935	-4.0	-0.8	-3.8	58.7

v = loaf volume. 2 = bran frost. 3 = heavy frost. 4 = immature. 6 = protein content.

The multiple correlation coefficients showing the combined relation of protein and the different classes of damage with loaf volume (Table XI) are higher than any of the other correlations studied, and they show that from 60% to 98% of the variance in loaf volume, depending on the year, can be predicted from a knowledge of the protein content and the percentages of bran frosted, heavily frosted and immature kernels in the sample. This would be sufficiently close for grading purposes, but this level of accuracy can only be attained if the relation of these factors to loaf volume is known in advance. The great variability in the partial regressions (Table XII) makes it impossible to arrive at even a reasonable estimate of the relative effect of these factors on the basis of the experience of past years, and an actual determination of the partial regressions which could not be made before the crop year is well advanced would only be of academic interest.

The variation in the partial regressions of loaf volume on protein and the known differences in the general character of the damage in different years (Table I) made it seem possible that the relation is a complex one worthy of further study. Accordingly, the simple regression coefficients of loaf volume on

protein content were calculated for each grade and year and are given in Table XIII, and graphically, for the bromate formula only, in Fig. 1. In 1930 and 1932 the differences between the regression coefficients are highly significant. For the bromate formula in 1931, for the malt-phosphate-bromate formula in 1934 and for both formulas in 1935, they are just above the 5% level of significance and the remainder of the differences are not significant. In addition, there are some marked differences between the regression coefficients for the same grade and formula in different years. The graphs show that the regression lines differ not only in slope but also in general level.

TABLE XIII
RELATION OF PROTEIN CONTENT OF WHEAT AND LOAF VOLUME BY GRADES

Year	Simple regression coefficient, cc. per 1%				Significance of differences between regression coefficients	
	3°	4°	No. 5	No. 6	F	5% point
<i>Bromate formula</i>						
1930	40.9	38.6	83.8	85.6	5.27	2.79
1931	74.9	36.2	64.0	97.6	3.09	2.79
1932	42.6	61.0	61.9	124.0	6.35	2.79
1933	52.1	66.4	39.3	57.2	0.80	2.79
1934	63.7	56.3	64.8	50.7	1.04	2.74
1935	47.4	57.8	67.6	21.0	2.81	2.74
<i>Malt-phosphate formula</i>						
1930	28.5	17.2	66.9	76.0	5.13	2.79
1931	40.0	7.1	33.1	55.0	1.28	2.79
1932	3.8	40.3	47.9	120.8	16.61	2.79
<i>Malt-phosphate-bromate formula</i>						
1933	62.8	74.0	45.2	64.8	0.78	2.79
1934	89.2	85.2	87.2	58.0	3.26	2.74
1935	55.2	63.9	76.7	23.8	2.77	2.74
<i>Blend bromate formula</i>						
1930	20.1	22.3	39.8	45.8	2.20	2.79
1931	35.0	4.8	25.3	49.2	3.14	2.79
1932	35.0	31.0	30.1	63.5	2.80	2.79
<i>Blend malt-phosphate-bromate formula</i>						
1933	25.2	29.7	19.0	35.6	0.99	2.79
1934	35.0	35.4	39.2	25.8	2.53	2.74

The differences in slope might be the result of differences in the damage distribution over the protein range for different grades. This was checked by calculating the simple correlation and regression coefficients of the percentage of heavily frosted and immature kernels on protein content. In 1931, No. 5 gave a correlation of -0.45 with a regression of -10.4 , indicating that the line shown for this grade on the graph slopes more steeply than it would if the protein-damage distribution were uniform. The other lines are unaffected.

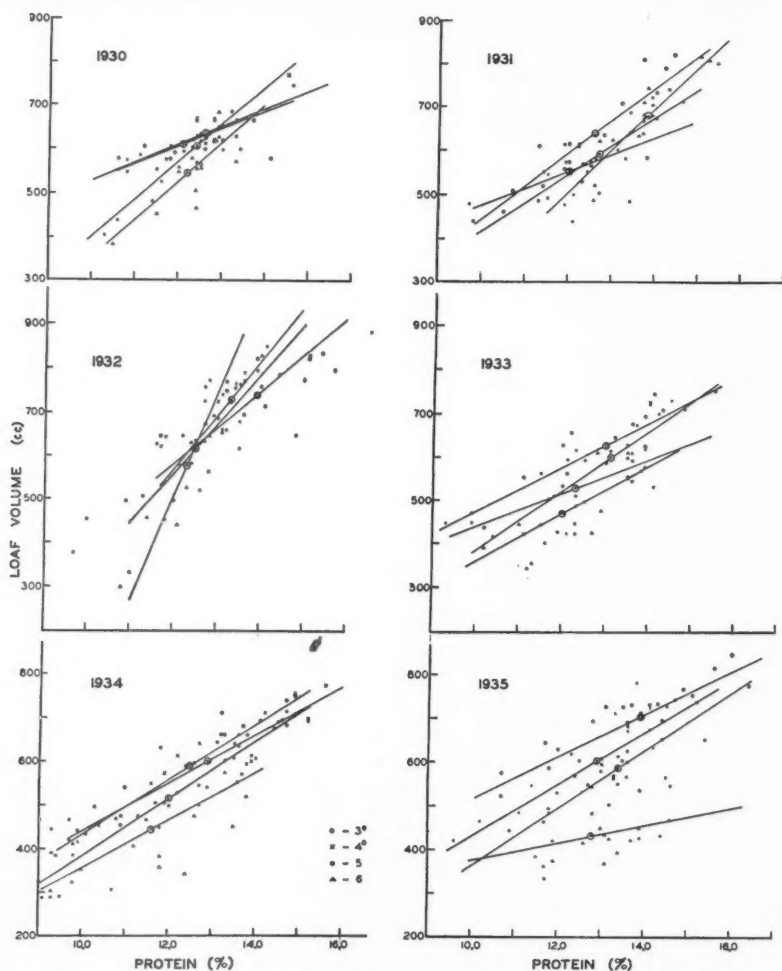


FIG. 1. Simple regression of loaf volume and protein content (bromate formula).

Provided that gas production is not a limiting factor, the differences in slope and level of the lines of regression of loaf volume on protein quantity must be related to differences in the protein quality in the widest sense of this term, including not only the character of the protein as originally present in the flour, but also the factors which may modify this character during fermentation. The bromate formula does not guarantee adequate gas production, but the similarity in character of the regression diagrams obtained with the malt-phosphate and malt-phosphate-bromate formulas and those for the bromate formula indicates that gas production was not a limiting factor. The relation between the slope and level of a regression line and protein quality is complex and direct interpretation is not easy. If two regression lines have different general levels the lower one must represent a lower protein quality, as equal quantities of protein do not produce equal loaf volumes. If lines have different slopes it indicates that the relative protein quality changes with the amount of protein present, or that the quality represented by the steeper line is so poor that gas retention is deficient in the lower protein range. One might hazard a guess that where the general levels differ the characteristics of the protein as originally present in the flour are different over the entire protein range and, in the second case, that the deleterious factors operative in the dough are different in kind or degree, and when the protein content is sufficiently high the net deleterious effect is not as serious as when the protein content is so low that good colloidal character would be necessary to maintain normal expansion. We have no experimental evidence to support this hypothesis, but the fact that none of the regression lines have a negative slope is not inconsistent with it. In the actual regression diagrams, of course, both slope and level may differ simultaneously.

In an attempt to relate the character of the regression lines to the physical character of the samples the multiple regression of these regression coefficients on the average percentage of bran frost, heavy frost and immature kernels for each grade was calculated but was found to be insignificant. However, the coefficient for heavy frost was considerably higher than for the other two classes of kernels and the simple correlation between this kind of damage and the regression of loaf volume on protein content for each grade was found to be 0.53, with a regression coefficient of 0.51, both of which are statistically significant. Thus we can conclude that the slope of the line representing the relation between protein and loaf volume in each grade becomes steeper as the average amount of heavy frost damage increases, and that the effect of bran frost and immature kernels is negligible. In other words, heavily frosted kernels have an effect on "gluten quality" which is markedly deleterious to loaf volume when the protein content is low, and less evident, or even absent, when the protein content is high.

Since a large proportion of Canadian wheat is used for blending it is of interest to ascertain the effect on this relation of the reduction of protein content by blending. The simple correlation and regression coefficients describing the relation between the coefficients of the regression of loaf volume

on protein content derived from the results of the bromate and malt-phosphate-bromate tests, and those derived from the corresponding blend tests, were found to be $r = 0.80$, $b = 0.40$, both of which are highly significant. The variation with protein content in the effect of heavily frosted kernels can be seen in blended flour, but its magnitude is reduced roughly in proportion to the amount of weaker flour used in the blend.

In the last three years of the survey the differences between the slopes of the regression lines are insignificant, or just barely significant, while there are pronounced differences in their general level, and thus we were able to study the relation of the different forms of damage to the level of the loaf-volume-protein regression lines, relatively freed from the complication of differences in slope. The level of each regression line was taken as the loaf volume at the point of intersection of the regression line with the ordinate for the average protein content of all samples in that year. Grade 3 Northern was taken as standard and the levels expressed as differences between this grade and No. 4 Northern, No. 5 and No. 6, for each year, and correlated with the corresponding differences in the percentage of immature kernels, giving a correlation coefficient of $+0.83$, which is highly significant. It appears that immaturity has a detrimental effect on "gluten quality" which is independent of the amount of protein.

Thus there are three factors which can be used simultaneously as an indication of the loaf volume—protein, percentage of immature kernels and percentage of heavily frosted kernels. Since it has been shown that immaturity and heavy frost are both related to gluten quality these factors should also give an indication of the wider character, baking quality, including dough characters and the shape and texture of the loaf. This receives support from the general relation which can be seen in Table I and Table III, and from the significant simple correlation (0.59) between the sum of the percentages of heavily frosted and immature kernels and the texture score which was calculated, 3 Northern being used as a standard in a similar manner to that given in the last paragraph. The crumb color score is also affected by these forms of damage.

TABLE XIV
RELATION BETWEEN YIELD OF
STRAIGHT FLOUR AND LOAF
VOLUME (BROMATE FORMULA)

Year	Simple correlation coefficient	5% point
1930	.58	.25
1931	.08	.25
1932	.70	.25
1933	.48	.25
1934	.67	.22
1935	.63	.22

COMBINED MILLING AND BAKING QUALITY

The grade ought to give an indication of both milling quality and baking quality and it is important to ascertain whether specifications ensuring a good indication of the one can be consistent with good indication of the other. Milling quality is related to weight per bushel, and to the percentages of heavily frosted and immature kernels. Baking quality is related to protein content and the percentages of heavily frosted and immature kernels. Thus there are two common factors and a third (test weight) which is related to these two. There should,

therefore, be a fair degree of correspondence between the variation in the two qualities. The simple correlations between yield of straight flour and loaf volume (Table XIV) are highly significant, with the exception of that for 1931, and this should facilitate the simultaneous indication of milling and baking quality by a single grade designation.

Discussion

The system of grading frosted wheat on the basis of the weight per measured bushel and the nature and extent of the damage to the appearance of the kernels is applied by the inspectors of the Western Grain Inspection Division in a satisfactory manner. Any major weaknesses in the grading of this class of Canadian wheat cannot be attributed to deficiencies in the application of the system.

The average milling quality of frosted wheat decreases with grade in every year, but there are marked discrepancies in the baking quality. However, with the exception of 1931 the average combined milling and baking value decreases as the grade lowers, though the spreads between the grades are by no means uniform. If the system were perfect, both milling quality and baking quality should decrease regularly from grade to grade when the average of the crop is considered. This ideal is far from being realized. There is great variation in the quality of the individual samples entering into any grade, and this variation is more pronounced in the baking quality than in the milling quality, and might even be described as excessive. In practice this situation means that the importer purchasing large bulk lots of frosted wheat has much more assurance that the grade will be a true indication of the combined milling and baking quality than has the farmer delivering a single wagon or carload, because the former quantity approaches more nearly the average of the grade for any crop year. The grading of individual frosted samples stands in great need of improvement, particularly in bringing the grade in harmony with the baking quality. If this can be done the regularity in quality of export would also be improved.

The avenues by which improvement might be sought are strictly limited by practical considerations. Speed is a necessity in the grading of Canadian wheat. On October 1, 1928, the Western Grain Inspection Division graded 3,787 cars of grain in a single day, and the inspections of wheat at Winnipeg alone commonly number 1,700 per day during the rush season. Simplicity of method and equipment and reasonable cost of the latter are highly desirable, as unofficial grading by the operators is necessary for a substantial portion of the grain handled by nearly 6,000 country elevators. No method of testing wheat which cannot meet these requirements is worthy of consideration as a basis for grading. This rules out the Brabender Farinograph or methods similar to the Pelshenke test, and in addition these methods have been shown to be unsatisfactory, even in the hands of skilled technicians, when used with Canadian hard red spring wheat (1, 4). Furthermore, any radical change in the basis of grading would lead to a period of confusion in

the trade until the precise effect of the change was thoroughly understood by all interests. These considerations led us to the view that the factors now in use should be utilized so far as possible.

The most satisfactory indications of the milling quality of frosted wheat can be obtained either from the weight per measured bushel or from the percentages of heavily frosted and immature kernels. The latter class of damage is somewhat more deleterious than the former. The test weight is influenced in a similar manner. Some improvement in the indication of milling quality might be effected through the adoption of stricter limits for test weight. To estimate the baking quality three factors must be used: protein content, and the percentages of heavily frosted and immature kernels. The use of damage alone as at present is not satisfactory; on the other hand, while protein is the best single index of baking quality, the relation is improved if damage is taken into account. Immaturity is equally undesirable over the entire protein range, but the bad effect of heavy frost in a sample is comparatively small if the protein content is high, and very pronounced if the protein content is low; this relation persists even when the protein content is reduced by blending. It is probable, in the light of the work of Newton and McCalla (9), that the protein content gives a rough indication of what the baking quality would have been if the sample had been mature and unfrozen; while the physical appearance of the kernels is related to the decrease from this quality level due to frost injury. The presence of immature kernels in a sample has a double significance since immaturity is deleterious, even without frost, and the harmful effect of frost increases with the immaturity of the wheat at the time of freezing (10). The percentage of immature kernels increases, in a general way, with both immaturity at freezing and the severity of the frost (8).

It will be noted that two of the factors are related to both milling quality and baking quality. This is most fortunate as it greatly facilitates the simultaneous evaluation of these two characteristics which differ so greatly in their nature.

The complete application of these findings in practice is dependent on the protein content being made a factor in the grading of wheat. The introduction of a protein requirement in the grade specifications, or even its indication as a notation on the certificate is fraught with very great difficulties (6, 7) and it does not seem that the advantages to be gained would compensate for the expense and complication of trade practice involved. However, there is another possible method by which the protein content could be taken into account. The wheat-growing region of Western Canada can be divided into zones: the open prairie, and the area where gray-wooded soils predominate, lying mostly in the northern section of the Western Provinces, with a transition zone between these two. The annual protein surveys of the Laboratory of the Board of Grain Commissioners (2) have established that the protein content of wheat in the first zone is generally high and that of the second definitely lower. The separation of the two main zones for grading purposes

would greatly facilitate the evaluation of quality from the appearance of the samples. This proposal will require careful and detailed study, but the use of a zoning system in Argentina is evidence that it is not outside the range of practicability. It is not feasible, of course, to apply a zoning system for the grading of frosted wheat alone, and its application to this class of wheat would have to be considered as part of a general revision of the wheat-grading system. A discussion of this wider problem is beyond the scope of this paper.

Of the factors now in use the greatest importance should be attached to the percentage of immature kernels, with somewhat lesser emphasis on the percentage of heavily frosted kernels. The percentage of bran frost can be disregarded because if this form of damage is present alone it indicates that the frost to which the grain was exposed was not severe and that it occurred late in the development of the plant and, consequently, there was no real injury to either milling or baking quality (10); if, on the other hand, a sample contains, in addition, heavily frosted and immature kernels, these forms of damage are the only ones that need be considered. The weight per measured bushel, which is always determined in grading, can be used to supplement the estimation of damage. While refinement in the application of the present grading factors might effect a minor advance, no major improvement can be expected unless the protein content is taken into account.

The results of the six years' survey are essentially in agreement with those of the study of the 1928 crop (5). The importance of the protein content as a measure of baking quality and the utility of weight per measured bushel as an index of milling yield are common to the conclusions from both investigations. In the present study the significance of the percentages of heavily frosted and immature kernels was elucidated through the use of methods of statistical analysis inapplicable to the results of a single year, and our earlier conclusion that the proportion of sound kernels was just as informative as the percentages of the individual forms of damage has, therefore, been revised.

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THE MALE GENITALIA IN THE HYMENOPTERA (INSECTA), ESPECIALLY THE FAMILY ICHNEUMONIDAE¹

II. TAXONOMY OF THE ICHNEUMONID GENITALIA

By OSWALD PECK

Introduction

During the last twenty-five years, there has been considerable disagreement upon the identity of the type species of some of the early ichneumonid genera and, therefore, upon their correct generic names (28, 31, 73, 103, 104, 134, 136). The merits of some of these proposed names are at present under the consideration of the International Commission upon Zoological Nomenclature (125); the names used in this study are therefore those consecrated by time and employed by Schmiedeknecht (114-117). This is of advantage also in that the majority of the species studied in this paper are European.

The classification of the Ichneumonidae is also still unsettled. The most recent complete classification is that of Schmiedeknecht (114). This has been brought further into line with recent thought by his unfinished series of fascicles, supplementing his *Opuscula Ichneumonologica*; in these he has adopted some of the concepts of Cushman and Rohwer (32), dividing the tribe Pimplini (*s.l.*) (116).

The generic limits of many ichneumonid genera are very indefinite at the present time and this condition is clearly shown in this study, where both holarctic and nearctic species are used. As an example, the nearctic species of the genus *Ichneumon* L. (*i.e.*, *Amblyteles* Cush. *et al.*) frequently cannot be placed with certainty within any of the genera or subgenera recognized by European workers (30, 81), although Cresson (25) attempted to do this. Cushman's concept of the genus *Ichneumon* has been retained. Too, the genus *Hemiteles* of Schmiedeknecht (114, 115) was considered by him as a single unit, for the sake of convenience. It is a very large group, susceptible to subdivision, as shown by Roman (102) and Cushman (30). Similarly the genus *Pimpla*, as recognized by Schmiedeknecht (114), is now divided into a number of subgenera or genera (30, 116).

When possible, the type genus of each tribe was selected for study. While, from the systematic viewpoint, the type genus should be studied whenever possible, yet, when material is scarce, the substitution of another genus may not be always detrimental and, in some cases, even advantageous. The type genus was arbitrarily created the nomenclatorial representative of a higher

¹ Concluded from November issue.

group, although possibly atypical. The type species is the systematic representative of a group but that is no criterion of its possession of the morphological attributes primitively common to the majority of that group. While in theory the characteristics of a group should be shown by a graduated series, in practice such thoroughness is often limited by time, material, and expense in publication.

These limitations have prevented any close study of specific differences, so that variations termed specific may prove to be only intra-specific. The practical restraints of material also preclude the thorough testing of any taxonomic inferences, therefore suggestions of this nature must be regarded as *purely tentative*, requiring the evaluation of the intensive systematist. This is needed also because the author claims no intimate knowledge of the various groups within the ichneumonids.

In order to aid the systematist to evaluate the data presented in this paper, the names of the ichneumonid species studied are listed below, the genera and species being grouped alphabetically in their respective tribes and subfamilies as recognized by Schmiedeknecht (114), subject to his revision of the Pimplinae (115). Cushman's division of the Pimplini (29) has also been indicated. Since the name *Ephialtes* L. is here used in the traditional sense for certain members of the Pimplini, all species of *Ephialtes* Cush. are referred to by his subgeneric name *Itoplectis*, here used with generic status merely to avoid a confusion in names.

Ichneumonidae

1. ICHNEUMONINAE

A. Joppini

Trogus lutorius Fabr.

B. Ichneumonini

Ichneumon animosus Cress.; *Ichneumon grotei* Cress.; *Ichneumon longulus* Cress.; *Ichneumon perscrutator* Wsm.; *Ichneumon variegatus* Cress.; *Neotypus americanus* Cush.

C. Phaeogenini

Phaeogenes gaspesensis Prov.; *Phaeogenes hariolus* Cress.

D. Alomyini

Alomyia debellator Fabr.

2. CRYPTINAE

A. Stilpnini

Atractodes sp.

B. Phygadeuonini

Glyphicnemis crassipes Prov.; *Microcryptus basizonius* Grav.; *Neostricklandia sericata* Cush.; *Stylocryptus subclavatus* Say.

C. Hemiteliini

Cecidonomus inimicus Grav.; *Hemiteles (Astomaspis) fulvipes* Grav.; *Hemiteles (Astomaspis) submarginatus* Bridgm.; *Hemiteles (Hemiteles) hemipterus* Fabr.; *Hemiteles (Hemiteles) subzonatus* Grav.

D. Pezomachini

No representative.

E. Cryptini (including Mesostenini)

Acronicus junceus Cress.; *Cryptus sexannulatus* Gr.

3. PIMPLINAE

A. Lissonotini

Cylloceria sexlineata Say; *Lissonota varia* Cress.

B. Glyptini

Glypta fumiferanae Vier.; *Glypta rufiscutellaris* Cress.

C. Lycorini

No representative.

D. Phytodietini

Phytodietus annulatus Prov.

E. Theroniini

Theronia fulvescens Cress.; *Theronia melanocephala* Cress.

F. Polysphinctini

Polysphincta sp. (*P. venator* De Gant?); *Zatypota percontatoria* Grav.

G. Labenini

No representative.

H. Rhyssini

Megarhyssa citraria Ol.; *Megarhyssa greeni* Vier.; *Megarhyssa lunator* Fabr.; *Rhyssa persuasoria* L.

I. Acoenitini

Phaenolobus arator Rossi

J. Xoridini

Deuteroxoides vittifrons Cress.

K. Odontomerini

Odontomerus canadensis Prov.; *Odontomerus pinetorum* Thoms.

L. Pimplini

(a. Pimplini Cush.)

Ephialtes (*Calliephialtes*) *grapholithae* Cress.; *Ephialtes tuberculatus* auctt. Angl. nec Fourc.; *Exeristes roborator* Fabr.; *Pimpla brevicornis* Grav.; *Pimpla* (*Iseropus*) *coelebs* Walsh; *Pimpla detrita* Holmgr.; *Pimpla examiner* Fabr.; *Pimpla instigator* Fabr.

(b. Ephialtini Cush. and Roh., nec auctt.)

Apechthis ontario Say; *Itoplectis* (*Ephialtes* Cush.) *pedalis* Cress.; *Itoplectis* (*Itoplectis*) *conquisitor* Say; *Itoplectis* (*Itoplectis*) *obesus* Cush.

4. TRYPHONINAE

A. Mesoleptini

Hadrodactylus typhae Geoffr.; *Lagarotus insolens* Grav.; *Lophyropsectus luteator* Thunb.; *Mesoleius multicolor* Grav.; *Mesoleius tenthredinidis* Morl.; *Perilissus* (*Spanotecnus*) *filicornis* Grav.

B. Tryphonini

Erromenus crassus Cress.; *Tryphon incestus* Holmgr.

C. Cteniscini

Exenterus canadensis Prov.; *Exenterus claripennis* Thoms.;
Exenterus lepidus Holmgr.; *Exenterus marginatorius* Fabr.

D. Paniscini

No representative.

E. Bassini

Bassus tricinclus Grav.; *Homotropus pectoratorius* Grav.

F. Orthocentrini

Orthocentrus sp.

G. Exochini

Exochus sp.; *Triclistus curator* Fabr.

H. Metopiini

Metopius sp.

5. OPHIONINAE

A. Ophionini

Enicospilus ramidulus Grav.; *Ophion obscurus* Fabr.

B. Nototrachini

Nototrachys foliator Fabr.

C. Ophionellini

Hymenopharsalia foutsii Cush.

D. Anomalonini

Agrypon flaveolatum Grav.; *Anomalon flavifrons* Grav.; *Exochilum circumflexum* L.

E. Campoplegini

Diocles obliteratus Cress.; *Inareolata punctoria* Rom.; *Omorgus borealis* Zett.; *Omorgus ensator* Grav.; *Omorgus mutabilis* Holmgr.

F. Cremastini

Cremastus (Cremastus) flavo-orbitalis Cam.; *Cremastus (Cremastus) geminus* Grav.; *Cremastus (Cremastus) interruptor* Grav.; *Cremastus (Cremastus) minor* Cush.; *Cremastus (Zaleptopygus) incompletus* Prov.; *Demophorus robustus* Brischke; *Pristomerus vulnerator* Panz.; *Pristomerus appalachianus* Vier.

G. Porizonini

Orthopelma luteator Grav.

H. Plectiscini

No representative.

I. Banchini

Banchus falcatorius Fabr.; *Exetastes fascipennis* Cress.; *Exetastes fornicator* Fabr.; *Exetastes matricus* Prov.

J. Mesochorini

Mesochorus pectoralis Ratz.; *Cidaphus occidentalis* Cush.

The Value of the Genitalia in the Order Hymenoptera

The male genitalia have been widely used for taxonomic purposes in the principal pterygote orders, including the Hymenoptera. Among the latter group these appendages have been invaluable in some aculeate families, although they have not been used extensively in the Chalastogastra and Ichneumonoidea.

The ignoring of the male genitalia in these lower groups does not seem to be due to a lack of suitable characters, for the diversity of form has been shown by both Crampton (22) and Boulangé (17). Crampton, however, drew no systematic conclusions and did not include any specific studies but, when his work is compared with that of Boulangé, it is evident that good specific characters occur in *Cimbex*, *Xiphidria*, *Tenthredo*, *Dolerus* and *Cephus*, a wide representation of the Chalastogastra. Boulangé (17) considered the aedeagus to be the best source of specific characteristics, and Benson (9) found the shape of the ninth sternum in the tenthredinid genus *Athalia* to be specific in value, while the gonosquamae and parapenes were used by Rohwer (99) to separate the tenthredinid genera, *Lagium* and *Zalagium*. Among the nearctic sawflies, the genitalia are characteristic in some genera of the Allantinae (107), in species groups of *Dolerus* (105) and in individual species in *Empria* (106).

The separation of the Oryssidae from the Chalastogastra is supported by the radical difference in the resting position of the genitalia, those of the former always being concealed (38, 98), while those of the latter are infrequently so.

Differences have been observed among the ichneumonids, more especially the elongate gonosquama of *Banchus*, *Hemiteles nanus* Grav., *Lathrolestes* Foerst. and *Parabates* Foerst. (82), as well as those of the Mesochorini (21, 82, 114). The genitalia of *Amblyteles* sp., *Cryptus* sp. *Ichneumon lineator* Fabr., *Pimpla roborator* Fabr., *Psilosage ephippium* Holmgr. (a tryphonine) and *Metopius dissectorius* Panz. are dissimilar (21), as are those of *Hemiteles hemipterus* Fabr., *Collyria calcitrator* Grav. and *Pimpla detrita* Holmgr. (109), while those of *Calliephialtes* sp. (26) and of *Mesostenus* sp. and *Tryphon* sp. (8) differ again from each other.

The workers upon the aculeate groups have used the male genitalia extensively, especially in the Apoidea (87), Colletidae (72, 91), Andrenidae (5, 48, 49, 92, 112); Megachilidae (67-69), Bombidae (59, 86, 94, 95), Pompilidae (89), Chrysididae (90), Vespidae (10, 58), Tiphidae (3, 60), Mutillidae (64, 65, 88) and the Sphecoidea (77, 78, 83, 93). Most of these workers confined themselves to a study of the hypandrium and of the undissected genital parts and found that the hypandrium and the apices of the outer claspers, of the inner claspers and of the aedeagus were extremely valuable in the identification of species. The situation seems to be adequately summed up by Mickel (65), who states, in reference to the Mutillidae, that:—

"the genitalia of the male have proved of inestimable value in settling certain points, especially in groups of males that are superficially alike. It has been possible to determine that certain external characters were of specific value by using the genitalia as a criterion. On the other hand, certain groups

of males quite different in superficial appearance possess genitalia that are practically identical, so that these structures have been of assistance not only in the distinguishing of species, but also in determining the relationships of species, which is exceedingly important from the viewpoint of phylogeny."

As a consequence of the extensive specific differentiation, the occurrence of generic and supra-generic characters seems to be rare. Hagens (48) suggested such for groups among the Apoidea but they do not appear to be well substantiated by his data. Parker considered the posterior spines of the hypandrium in some Bemicini as generic, while the shape of the spatha served to distinguish all but two of the twelve American genera (77, 78). The presence of the pygopods has been used by both Saunders (112) and Radoszkowski (93) as the first step in separating the Sphecoids, although in the Lasiini (Formicidae) it is of generic interest (37). A marked similarity of the genitalia was noted among the Pseninae (Sphecidae) and among the Tiphidae, although the apical portions are subject to specific variation (61). This similarity is true also of many other groups; for example, the gonoforces of *Andrena* and *Halictus* (Apoidea), as illustrated by Atwood (5), seem to form two very distinct groups, although they are closely related. There thus appear to be reasonable grounds for suspecting that generic and possibly super-generic characters are present in the ichneumonid genitalia. Such an occurrence may be true in the Sphecoidea, for a key to the group was made by Radoszkowski (93), using chiefly the form of the inner clasper, the parapenial area and the gonosquama. However, few species were used in this key.

The existence of these higher characters is suggested also by the work of Boulangé (17), who stated that the basal portions of the chalastogastrous genital sclerites were of greater value in determining the larger groups than were the apices, owing to the restraint placed upon differentiation by the muscular attachments. Should this be so, it is not surprising that few characters of the higher denominations have been found, since most of the workers cited appear to have studied the genitalia as an undissected unit.

In contrast to these views, Richards (94, 96) holds that (i) almost any sclerites are liable to differentiation in the genus *Bombus* and (ii) in each of the main divisions of the aculeate groups, specialization takes place through fusion and, as this may occur within a family or even within a genus, it is not possible at present to use the male genitalia to any great extent in classification. While these views are not diametrically opposed to those of Radoszkowski, yet they do suggest that Radoszkowski's may need considerable modification and possibly even rejection.

Considering the evaluation of the genitalia in other hymenopterous groups, it seems probable that among the Ichneumonidae (i) there are numerous specific differences, occurring chiefly among the apical portions of the sclerites, (ii) generic and suprageneric characters are rare, to be found probably in the basal parts of the sclerites and (iii) if the differences involve fusion, then they may be regarded as abnormally variable. The work of Ceballos (21) and Salt (109) shows that Berthoumieu (12) was incorrect in believing that there

are no significant differences in the ichneumonid genitalia, but the former workers make no suggestion as to the possible taxonomic value of these structures.

The purpose of the taxonomic portion of this paper is to estimate the amount of variation that occurs in the genitalia of the ichneumonid males. The differences may be of real practical value, the quoted findings of Mickel (65) upon these structures in the mutillids then being perhaps equally applicable to the ichneumonids. On the other hand, the ichneumonid genitalia may be merely concealed structures, their differences only separating groups or species that are already readily recognized. This practical evaluation of the genital structures, however, must be left to the intensive systematist, only the type of variation being shown in this paper.

The Genital and Postgenital Terga among the Ichneumonids

As shown above, the hymenopterous gonotergum slowly evolved from the form of the pregenital tergum, first as gonotergites and subsequently as either a syntergum or a pair of syntergites, the syntergites later degenerating. This series of modifications occurring gradually in the Hymenoptera suggests that these structures should possess characters of value in identifying large groups within the ichneumonids, although the conclusions of Richards (96) in regard to the fusion of sclerites in the aculeates suggest otherwise.

Within the Ichneumonidae, the gonotergum is apparently always divided and it may be fused to the tenth tergum; the latter may be split into a pair of lateral tergites, although there is no significant reduction in the size of the syntergites. Unfortunately, these changes are not linked to the larger groups, for the inherent tergal characters, if present, appear to be concealed or partially masked by other influences, these being probably either the depressed or compressed shape of the abdomen, or the variations in the proportions of the hypandrium and of the gonopods, or both.

When compared with the specific variation of the hypandrium and the genital appendages, the compression or depression of the abdomen may be considered as distinctly inherent and, if so, there should be a correlation between the gonotergal form and the extreme knife-edge type of compressed abdomen. Among the ten most suitable species of the latter type (taken without regard for taxonomic considerations), *Ophion obscurus*, *Enicospilus ramidulus* and *Anomalon flavifrons* (all closely related), as well as *Hymenopharsalia foutsii*, have synterga, while *Acrornicus junceus*, *Banchus falcatorius* and *Lophyroplectus luteator* have syntergites; *Cremastus* spp., *Agrypon flaveolatum* and *Exochilum circumflexum* have a syntergum that is partially separated medianly. Evidently, if abdominal shape is an inherent factor in the modification of the genital tergum, it is completely dominated by more superficial characters and can be ignored.

The specific characteristics of the ninth and tenth terga are found in (i) the general proportions, (ii) the degree of inter-tergal fusion and (iii) the degree of the division in the tenth tergum.

Proportional variations appear to be common, some being shown in the lateral views of species belonging to the genera *Glypta*, *Theronia*, *Exetastes* and *Exenterus* (Figs. 23–30).

The degree of fusion between the terga may vary specifically, as shown in the complete fusion in *Glypta fumiferanae*, although this is incomplete anteriorly in *G. rufiscutellaris* (Figs. 23, 24). The latter condition is found also in *Cecidonomus inimicus*, while the closely related *Hemiteles* species have the intertergal fusion completed.

The division of the tenth tergum is not always uniform within a genus. *Cremastus* has a series of species that includes synterga, almost completely separated syntergites and intermediate forms (Figs. 31–34). In *Itopectis conquisitor* the syntergum is completely fused medianly but in *I. obesus* it is incompletely so, while the syntergites of *I. pedalis* have completely fused intersegmentally. Similarly a wide variation occurs in *Pimpla*, since *P. examinador* and *P. instigator* possess synterga, and *P. brevicornis* syntergites with incomplete intersegmental fusion, while *P. detrita* and *P. coelebs* have separate tergites in both terga (Fig. 21). *P. detrita*, however, has been placed in *Epiurus* by Roman, as cited by Salt (109).

Apart from the exceptions already noted, the terga in each genus are of one type only. It is possible to consider three of the exceptions as heterogeneous genera, for *Cremastus* and *Pristomerus* have been divided into subgenera (27) and *Pimpla* contains both internal and external parasitoids (129). *Glypta*, however, is now considered as a homogeneous group. While great tergal variation occurs within the Phygadeuonini, Hemitelini, Pimplini, Cremastini, Pristomerini and Mesoleptini, yet in other tribes the tergal structures appear to be fairly uniform. Among the 22 species of the Ichneumoninae and Cryptinae (including 14 genera), 19 possess complete syntergites; however, two others, *Cecidonomus inimicus* and *Glyphicnemis crassipes* have the intertergal fusion incomplete, while the ninth and tenth terga of *Stilocryptus subclavatus* are divided into separate tergites. The terga of the other three subfamilies are remarkably varied, although tribally they show a uniformity of structure, apart from the exceptions already mentioned. The data are insufficient to show distinctly that the terga may be inherently constant within a tribe but, if this is so, then such uniformity of structure is usually either partially or entirely masked by specific differences.

During the study of the gonotergum, variations in the antecosta were seen, the anterior process in some Pimplinae being especially conspicuous. Since the antecosta is an internal ridge, serving as a place of attachment for muscles, it is unlikely that this structure would be greatly modified by the minor changes in the genitalia. The antecosta may therefore be a guide to the higher relationships of the ichneumonids.

No deliberate comparisons were made between the pretergal and gonotergal antecostae, yet they appeared to be similar, as is to be expected.

The genital antecosta may be (i) *linear* in form, as in *Exenterus marginatorius* (Fig. 30) (ii) *ovate* near the ventral margin, as in *Glypta rufiscutellaris* (Fig. 24),

or (iii) *appendicular*, a somewhat quadrate process projecting anteriorly from near the ventral margin of the antecosta, as in *Exeristes roborator* (Fig. 20) and *Itopectis conquisitor* (Fig. 35).

The tergal antecosta is linear throughout the Ichneumoninae, Cryptinae and Ophioninae, exclusive of a small process in *Hemiteles submarginatus* and an oval thickening in both *Mesochorus pectoratorius* and *Cidaphus occidentalis* (Mesochorini); the two latter exceptions stress the remoteness of the Mesochorini from the other tribes of the Ophioninae. *Exetastes*, too, is an exception, for in *E. matricus* and *E. fascipennis* the antecosta is lineo-ovate, although in *E. fornicator* it is linear; however, the genus is aberrant, being placed midway between the Ophioninae and the Pimplinae by Schmiedeknecht (117) and in the Lissonotini by Cushman (30).

The great uniformity of the antecosta among the Ichneumoninae, Cryptinae and Ophioninae is in strong contrast to the variation that occurs among the Pimplinae and Tryphoninae and emphasizes the heterogeneity occurring in the latter two.

Among the Pimplinae this diversity is indicated also by the primitively linear antecosta being characteristic of the Lissonotini, Odontomerini, Acoenitini and *Pimpla coelebs*, groups that are widely separated from each other. This suggests that they may be the primitive members of four different natural groups, more especially since these represent respectively the four original tribes of the Pimplinae, *i.e.*, the Lissonotini, Xoridini, Acoenitini and Pimplini as recognized by Gravenhorst (47), Holmgren (54), Ashmead (4) and Schmiedeknecht (114).

The ovate antecosta occurs in Glyptini and Phytodietini, while the pendant form is found in the Pimplini (*s.s.*), except *Pimpla coelebs*. The intermediate ovato-appendicular type occurs throughout the Theroniini, Polysphinctini, Rhyssini and Xoridini. The ovate forms suggest that the Glyptini and Phytodietini are moderately primitive, particularly since (i) strong lissonotine affinities have been noted in the Glyptini (Cushman and Rohwer (32)) and (ii) the Phytodietini have been grouped with the Lissonotini by Foerster (40), Ashmead (4) and Schmiedeknecht (114), although lately given tribal rank by Cushman and Rohwer (32) and Schmiedeknecht (116). Cushman and Rohwer (32), however, regard the Lissonotini and Glyptini as forming a group that is not at all closely related to the Phytodietini or to the rest of the subfamily, although akin to the Banchine *Exetastes*.

Cushman and Rohwer (32) also separate the Odontomerini from the Xoridini. *Odontomerus* spp. possess linear antecostae, while this structure is ovato-appendicular in *Deuterioxoides vittifrons*. Thus the tribe Odontomerini is more primitive than the Xoridini.

However, while the shape of the antecosta may assist in determining the tribal relationships within the Pimplinae, yet more data must be obtained before this structure is accurately evaluated in this group. The possibility of the antecosta being tribal in value is enhanced by its uniformity in the Ichneumoninae, Cryptinae and Ophioninae, the antecosta in the Tryphoninae also showing marked agreement with the taxonomic groupings.

Among the Tryphoninae the pendant antecosta occurs in the members of the Bassini, Metopiini and the Orthocentrini, although it was not seen in the Exochini. The first two tribes form the Tryphonides schizodonti and T. aspidopi respectively, while the latter two form the Tryphonides prosopi, these being supertribes recognized from early times by Holmgren (53), Morley (74) and Schmiedeknecht (114). The occurrence of a linear antecosta in *Exochus* sp. and an ovate one in *Triclistus curvator* (Exochini) perhaps indicates (i) that the Exochini are related to the Orthocentrini, being the more primitive portion of the supertribe, and (ii) that the antecosta is of tribal rather than supertribal value.

The majority of the Tryphoninae, however, occur in the Tryphonides homalopi, in which the antecosta varies from linear to lineo-ovate, the ovate form occurring rarely. Specific differences may occur, for in the four species of *Exenterus* studied, *E. canadensis* and *E. marginatorius* have an ovate antecosta, while *E. claripennis* and *E. lepidus* have lineo-ovate ones; it is difficult to know what weight to place upon these variations. However, it should be noted that the small number of Tryphoninae examined, together with the large number of subtribes recognized in this group does not justify any conclusions being drawn.

The same is perhaps true of all of the subfamilies, yet the shape of the antecosta in some groups is remarkably constant and does suggest that these basal structures may prove, upon closer study, to possess super-generic characteristics that are very seldom subject to masking by generic or specific variations. This possibility is augmented by the deplorable state of the taxonomy in this group, for, in view of this, it would indeed be surprising if the correlation between the antecostal form and the taxonomic opinions was higher, particularly since one cannot expect to be able to group the major divisions of any taxonomic group by employing merely one structure.

The Ichneumonid Hypandrium

As in most of the Hymenoptera, the posterior and lateral margins of the ichneumonid hypandrium is specific in value, this being shown in *Ichneumon*, *Phaeogenes*, *Hemiteles*, *Exelastes*, *Glypta*, *Theronia*, *Omorgus*, *Cremastus*, *Pimpla*, and *Exenterus* (Figs. 39-67). Desclerotization in the median line sometimes occurs, as in *Exelastes* spp., *Cremastus* spp. and in *Tryphon incestus* (Fig. 68). However, caution is advisable in the use of the shape of the hypandrium since intra-specific variations occur in *Exeristes roborator*; moreover, the curvature and outline of the ninth sternum can be altered by differences in the preparation of mounts. In *Megarhyssa*, there appeared to be no differences between the species, although the form in the genus is distinctive (Fig. 69).

While the greater portion of the hypandrium is specific in value, yet the antecosta with its median spiculum appears to be as significant as the tergal antecosta in revealing higher group characteristics, for there is a high negative correlation between the maximum width of the gonotergal antecosta and the

length of the spiculum—if the gonotergal antecosta is linear, the spiculum is long, and *vice versa*. This correlation is almost perfect in the Ichneumoninae, Cryptinae and Ophioninae, and is high in the other two subfamilies. Since the antecostae and spicula are only roughly classified, it is surprising that the correlation should be so high. In no case was a positive correlation found.

As a source of specific differences, the hypandrium appears to be the most promising of the sclerites in the genitalia and the genital segment, not only because it varies in form, but because many of its characteristics may be seen without dissection and because its large size usually permits a reasonably easy dissection to the novice.

The Ichneumonid Gonocardo

As noted above, the annular gonocardo is formed by the fusion of two lateral semicircular sclerites, each differentiated from the base of a gonopod. Among the ichneumonids these gonopodites are broadest ventro-laterally or laterally, their apices tapering towards the median line of the abdomen.

The ventral tips of these sclerites are almost invariably fused together as a narrow bridge. This area of juncture is always narrow, even when the gonocardo is unusually broad ventro-laterally, as in *Megarhyssa lunator* (Figs. 70, 71, 112) and *Banchus falcatorius* (Fig. 72). Medio-ventrally there is sometimes a small internal ridge or apophysis, presumably the remnant of a suture existing before the fusion was completed; these are noticeable in the more heavily sclerotized gonocardines.

The dorsal portion of these gonopodites varies greatly in shape. A complete annulus is typical of the Ichneumoninae and of the less specialized tribes among the Ophioninae, while in the other families the meso-dorsal apices are usually joined by membrane alone. Unfortunately these generalizations are not entirely true of all groups, for both *Neotypus americanus* (Ichneumoninae) and *Stylocryptus subclavatus* (Cryptinae) are exceptional. Furthermore, as these genera are typical of their respective subfamilies, it is likely that many exceptions will occur in groups intermediate to these larger groups.

An intergradation of these types also occurs in the Ophioninae. The gonocardo is completely annular in the less specialized tribes, including the Ophionini, Nototrachini, Ophionellini, Anomalonini, Campoplegini, Cremastini and Pristomerini. The species *Ophion obscurus*, *Agrypon flaveolatum* and *Exochilum circumflexum* (Figs. 73–75) may suggest a tendency for the primitive gonocardo to be medio-dorsally broad in the longitudinal direction, although this is not true of all, *Enicospilus ramidulus* (Fig. 85) having a fairly narrow dorsal bridge. The same region appears to be consistently very narrow in the intermediate tribes Cremastini and Pristomerini (Figs. 76–80) and to have degenerated into membrane among the highly specialized tribes, Banchini, Porizonini and Mesochorini (Figs. 72, 81, 82). It is of interest to note that the completely annulate gonocardo of *Hymenopharsalia* (Ophionellini) agrees with the position assigned to it by Cushman (29).

It should be noted that the Porizonini are represented only by *Orthopelma luteator*, the genus being aberrant and related to the Pimplinae (114), although placed in the Porizonini by both Schmiedeknecht (114) and Cushman (30). The remaining two specialized tribes, Mesochorini and Banchini, are also perhaps only placed provisionally in the Ophioninae. The Banchini may be related to the Lissonotini through the genus *Exelastes*, which is placed with the Banchini by Schmiedeknecht (114) and in the Lissonotini by Cushman (30). The remoteness of the genus has been emphasized by earlier taxonomists including Handlirsch (50), who created a subfamily for the genus; this attitude is supported by the occurrence of Braconid characteristics in the respiration of the banchine larvae (129). The Banchini have been regarded as remote, for Foerster (40) and Viereck (135) raised the group to family rank. The remaining group, the Mesochorini, is differentiated from almost all other Ichneumonidae by the extremely elongate outer claspers in the males (Fig. 82); the peculiarly flattened head and enlarged areolet are also highly characteristic. When the apparently consistent habit of hyperparasitism is also considered, it appears that the Mesochorini may merit elevation to the rank of supertribe.

Upon these grounds it is evident that the more specialized tribes of the Ophioninae possibly may not be true members of the subfamily and, if so, the Ophioninae are characterized by a completely annulated gonocardo. However there were not enough species available in these tribes for this to be determined.

While the gonocardo undoubtedly possesses characteristics common to large groups within the Ichneumonidae, yet this structure also shows definite specific differences. Viewed in cross-section, the ventral portion may be straight, as in *Ichneumon longulus* (Fig. 114) or incurved as in *I. variegatus* (Fig. 115). The gonocardo, when seen from below, frequently exhibits variation, the medio-ventral portion being either straight, curved anteriorly or curved posteriorly. The anterior curve is present in *Cremastus* spp., (Figs. 76-78) although the form of this portion of the gonocardo may vary specifically. Within *Ichneumon*, *Phaeogenes* and *Hemiteles* (*Astomaspis*) both the straight and the posteriorly curved forms occur, the former in *I. grotei* (barely curved), *P. hariolus* and *H. fulvipes* (Fig. 83) and the latter in the other *Ichneumon* spp. examined, in *P. gaspesensis* and in *H. submarginatus* (Fig. 84). In the examined species of *Omorgus* and *Exenterus* this area was invariably straight.

Among the Pimplinae also, the ventro-median portion of the gonocardo is of specific interest. *Megarhyssa citraria* is readily distinguished from the American species, *M. lunator* and *M. greeni*, by the antero-ventral notch in the former being but half the length and V-shaped without parallel sides (Figs. 70, 116). Within the genus *Pimpla*, too, this area possesses diagnostic characters. A prominent antero-median lobe distinguishes *P. brevicornis* from the other species that were examined. Some *Pimpla* species, including *P. examinator*, *P. instigator* and *P. detrita*, are exceptional among the ich-

neumonids, for the two lateral halves (*i.e.*, the basal gonopodites) have not fused ventrally; unfortunately, this has weakened the gonocardo, making it difficult for the unwarned to extract the genitalia without separating the two halves of the gonocardo. *Apechthis ontario* (Fig. 86) *Itoplectis conquisitor* and *I. obesus* are distinguished by the median portion being bent posteriorly as a broad "V" but this is not true of *I. pedalis*.

Yet, while the gonocardo may vary within a genus, the similarity of this structure in some genera, notably *Ichneumon*, *Megarhyssa*, *Glypta*, *Cremastus* and *Exenterus* suggest that these specific differences have not entirely concealed some characters of higher value.

The Ichneumonid Gonoforceps

The tribe Mesochorini is usually distinguished from other ichneumonids by its singular, extremely elongate gonosquamae, although this character is possessed also by *Ctenopelma sanguineum* Prov. (Tryphoninae) and by some or all of the Ophonellini. One might expect that the gonoforceps could be of use in identifying some of the larger groups. This, however, seems highly improbable, for while individual groups sometimes possess a common facies, yet only rarely, as in *Megarhyssa* and the *Mesochorini*, does one find that such facies are peculiar to one group.

This infrequency is due, at least in part, to the fact that each part of the gonoforceps may be differentiated specifically. The form of the gonostipital arm may vary within a genus, as in *Cremastus*, *Hemiteles* (*Astomaspis*), *Theronia*, *Glypta*, *Ephialtes* and *Exenterus* (Figs. 76-78, 83, 84, 87-96), as well as in *Ichneumon* and *Phaeogenes*. The main portion of the gonoforceps may vary in shape within a genus but seldom as radically as in *Ephialtes*, *Theronia* and *Exenterus*. The apex of the outer claspers often varies greatly within genera such as *Hemiteles*, *Glypta*, *Ephialtes*, *Cremastus* and *Exenterus* (Figs. 98-111).

The Ichneumonid Volsella

The ichneumonid volsella is a very flexible structure, this being necessitated by its function of finding, claspings and stretching the membrane lying adjacent to the female gonopore. Owing to this versatility of form in the individual, there seems to be no ideal method of mounting these structures without subjecting some part to possible distortion.

This part has been illustrated in several planes by Cushman (26), Becker (8), Ceballos (21) and Salt (109) and their works collectively show that it does vary considerably. However, as they dealt with thirteen species, representing eleven genera and all five of the traditional subfamilies, no taxonomic conclusions can be made from their work.

The typical ichneumonid volsella is similar to that of *Neotypus americanus* (Figs. 119, 120), the names of the parts being indicated in these figures. The area dorsal to the volsellar strut is termed, when present, the *dorsal area* of the volsella (D.A.), its margin almost invariably being supported anteriorly by the basivolsellar apodeme (Bv. A.).

While the volsella usually is completely separated by membrane from the gonoforceps, eleven exceptions were found, these representing four tribes in the Tryphoninae and one each in the Ichneumoninae, Cryptinae and Ophioninae. This character, therefore, appears to be widely spread, although intermittent. This peculiarity is evidently specific, at least in some groups, for a sclerotic tongue connects the antero-ventral part of the basivolsella to the gonostipes in *Ichneumon longulus* (Fig. 97), *I. grotei* and *I. variegatus*, although the volsella is free in *I. animosus* and in *I. perscrutator*. In the genus *Cremastus* also, *C. incompletus* and *C. geminus* have the volsella joined broadly to the gonostipes, although the other species examined in this genus have the volsella entirely separated. This latter condition is true also of *Neostricklandia sericata*, *Lagarotus insolens*, *Homotropus pectoratorius*, *Bassus tricinclus*, *Triclistus curator* and *Metopius* sp. The fusion in the last species occurs for more than half of the total length of the volsella.

Among the Ichneumoninae, excepting *Neotypus americanus*, the basivolsellar apodeme is large, curving ventrally (Figs. 121, 122), and this is true also of the species of *Atractodes* (Stilpnini) examined. Among the Phygadeuonini the apodeme is small but among the more specialized Cryptinae, such as *Hemiteles hemipterus* (Fig. 123), the apodeme is large and extended dorsally. To this *Hemiteles subzonatus* is an exception; for the apodeme is small and appears to be ventro-lateral.

The size of the dorsal area is closely correlated with the dorsal growth of the basivolsellar apodeme, for it is absent in the five *Ichneumon* species, scarcely present in *Alomyia debellator* and narrow in the other Ichneumoninae, as well as in *Atractodes*. Among the Phygadeuonini, the dorsal area is moderate in size, while it is well developed in the more specialized Cryptinae, such as *Cryptus sexannulatus* (Fig. 125). In *Glyphicnemis crassipes* (Phygadeuonini), however, the apodeme is small and does not support the large dorsal area. While this correlation is true also of *Neotypus americanus* and *Hemiteles subzonatus*, the former has a large dorsal area and the latter none, thus disagreeing with their present taxonomic position. This suggests that there is a closer correlation between the form of the apodeme and that of the dorsal area than between the shape of these structures and the taxonomic grouping within the Ichneumoninae and Cryptinae.

This conclusion also appears to be applicable to the other subfamilies, although, again, each subfamily has a strong tendency towards a particular type of apodeme with its corresponding form of the dorsal area.

Among the Tryphoninae, the basivolsellar apodeme is usually weakly developed, although it is strongly curved laterally in *Triclistus curator* and ventrally in *Erromenus crassus*.

In the Ophioninae the apodeme is invariably ventral. The dorsal area is usually absent, except in *Orthopelma luteator*, *Exetastes* spp. and *Enicospilus ramidulus*. The first species has the apodeme developed dorsally, while the dorsal area is large. However, as the genus *Orthopelma* is aberrant (114), this case may be disregarded. In *Exetastes* spp. the dorsal area is present,

although the apodeme is ventral and lateral; this genus is also aberrant (30, 114). In *Enicospilus ramidulus* (Fig. 124) the genitalia are unusually elongate so that this variation in volsellar form may be due to the need for reinforcement, for the apodeme is not of the normal dorsal type.

The form of the basivolsella divides the Pimplinae into two main groups, The Phytodietini being intermediate. The more specialized tribes are separated from the Lissonotini and Glyptini by the apodeme being well developed dorsally and by the great growth of the dorsal area. This agrees with the data upon the antecosta, which grouped together the Lissonotini and the Glyptini, as well as possibly the Phytodietini.

While the basivolsella is essentially a basal structure in which one may expect to find subfamily or tribal characters, yet it is also subject to generic or specific changes, not only in its fusion with the gonostipes, as already mentioned, but also in its proportions. The outline within some of the examined genera is similar, although specific differences may occur, as in *Ichneumon*. In this genus the narrowness of the basivolsella in *I. grotei* (Fig. 121) and *I. longulus* separates these species from *I. animosus* (Fig. 122), *I. variegatus* and *I. perscrutator*.

Among most of the Ichneumonidae, the apical portions of the volsella vary little from the type of *Neotypus americanus* (Figs. 119-120) although characters of specific value are to be found in the apex of the gonolacinia, for this may vary from being bluntly rounded, as in *Neotypus americanus* and *Glypta* spp. to being sharply pointed, as in *Ichneumon* spp. Within the genus *Ichneumon*, the length and shape of the gonolacinia varies, as shown in *I. grotei* (Fig. 121) and *I. animosus* (Fig. 122). A remarkable difference occurs in *Cremastus*, the gonolacinia being normal in both *C. minor* (Fig. 126) and *C. flavo-orbitalis*, although it is fused to the basivolsella in *C. incompletus* (Fig. 127) and *C. geminus*. This is of special interest as it emphasizes the fact that a character may appear to be extremely stable within the entire family although masked at times by a specific variation.

The Ichneumonid Aedeagus

The shape of the typical ichneumonid aedeagus is a weakly depressed cylinder, having the posterior apex curved somewhat ventrally and an elongate paramere extending anteriorly from each side. However, bizarre forms may occur within the family, as in *Agrypon flaveolatum* (Figs. 129, 141) and *Exochilum circumflexum* (Fig. 140).

The parameres are primitively joined to each other by membrane but the latter is often partially sclerotized, more particularly the dorsal or spathal area; this process is completed in some of the higher members of the Pimplinae, a medio-ventral fold (V.R.) being formed just in front of the apex (Figs. 70, 128, 134, 146-154). In most ichneumonids, however, this fold is membranous and allows the ventral portions of the valves to separate laterally. On this account the valves must be closed before comparisons are made in either the ventral or dorsal views.

The free anterior portion of the parameres is also subject to distortion, during treatment with potassium hydroxide, their shape therefore being of little taxonomic value. However, the anterior apex in *Hemiteles fulvipes* is dilated vertically, both upwards and downwards, in the form of a fishtail; in the other studied species of *Hemiteles* the paramere is rod-shaped, this being the almost invariable form in the Ichneumonidae. The length of the free portion may also vary specifically, as it is proportionately much less in *Ichneumon perscrutator* (Fig. 135) than in the other species studied in this genus (Figs. 136, 137).

These five species are readily divisible into three groups by their aedeagal shape. In both *I. grotei* (Fig. 137*) and *I. longulus* the aedeagus has small ergots and a dentate medio-ventral ridge, the ergots being long and the ridge without teeth in *I. variegatus* (Fig. 136), *I. animosus* and *I. perscrutator* (Fig. 135). The latter is readily distinguished from the others by the less falcate appearance and the shortness of the parameres.

All parts of the aedeagus seem to be differentiated specifically at times, as can be readily seen in *Hemiteles*, *Ichneumon*, *Phaeogenes*, *Glypta*, *Theronia*, *Ephialtes*, *Pimpla*, *Itopectis* and *Exenterus* (Figs. 83-84, 130-133, 135-139, 142-158). The diverseness in form between species must conceal and offset to a very great extent any intrinsic character of higher value, although some of the species within a genus do appear to have a facies common to the aedeagus.

Summary

(1) The muscles of the male genitalia (and of the adjacent parts) in the ichneumonid, *Megarhyssa lunator* F., are shown to be homologous with those occurring in other hymenopterous groups, especially the Chalastogastra.

(2) The median genital organ is an aedeagus. The volsella and gonostipes are derived from the same primary part of the gonopod. The gonocardo may represent the fused coxopodites and the claspers the telopodite; the ontogenetic and myological data are not in agreement but the latter is probably much diminished in value by the genital muscles being aided by changes in blood pressure.

(3) The term *gonolacinia* should be used for the apical sclerite of the inner clasper, as a substitute for the word *sagitta*. The latter, used originally for structures now identified as parameres, is frequently misapplied.

(4) The ninth and tenth terga in the Chalastogastra are but little modified but those of the Aculeata are small because of their invagination. In the ichneumonids, the ninth is invariably divided into a pair of lateral tergites; these may be fused to the tenth tergum which may also be divided medianly.

(5) The ninth sternum in both the Chalastogastra and Ichneumonidae is large, possessing an antero-median appendage, the spiculum. In the higher Hymenoptera, the ninth sternum is small and sometimes fused to the eighth.

*The names *I. grotei* and *I. variegatus* are interchanged on the illustration on page 251.

(6) Among the Ichneumonidae, almost every part of the genitalia (and of the adjacent parts) may be differentiated specifically. Variations that appear of value in identifying groups almost invariably have exceptions. While some of the latter may be due to misplacements of groups or species, the number of exceptions shows that specific variations mask characters of higher value to such an extent that the latter are unreliable.

(7) The form of the antecosta in the ninth tergum and the ninth spiculum may prove to have some value in the grouping of tribes. Unfortunately, these parts are not available for observation without dissection and treatment.

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STUDIES ON THE HETEROPHYID TREMATODE *APOPHALLUS VENUSTUS* (RANSOM, 1920) IN CANADA

PART III. FURTHER HOSTS¹

BY THOMAS W. M. CAMERON²

Abstract

Amia calva and *Ictalurus punctatus* are added to the list of carriers of the cysts of *Apophallus venustus* in the lower Ottawa Valley, and a probable human infection with the adult trematode is recorded.

Fish Hosts

During the summer of 1937, work was continued on the life history of *Apophallus venustus* with the result that two new fish have to be added to the list of carriers of the metacercaria given in Part II. of this series (1). These fish are the "fresh-water dogfish", "bowfin" or "lush" (*Amia calva*) and the "channel-cat" or "spotted catfish" (*Ictalurus punctatus*).

A number of specimens of both of those fish were caught by line in the Ottawa River, off Ste. Anne de Bellevue. As in the previous work, they were fed to cats which had been raised in the Institute and had not previously received any form of fish whatever.

The lush were not heavily infected but the catfish carried a considerable number of cysts. While it is not possible to give an exact comparison, they seem to be as suitable hosts as small-mouth black bass. This is of considerable interest as this species of catfish, like the bass, is an excellent food fish and a fair game fish. Various authorities rate it as being the most edible of fresh-water fish other than the Salmonidae.

Definitive Hosts

During the year, with the assistance of Dr. Angrove of the Ste. Anne de Bellevue Military Hospital, a considerable number of samples of human feces was submitted to the Institute for examination.

In one of these stools a number of eggs were found which agreed completely in shape and size with the eggs of *Apophallus venustus*. In spite of extensive search during the past three years no other trematodes of fish-eating mammals have yet been found in this neighborhood. Moreover, every species of this family of Trematodes, that has so far been tested in man, has found him a more or less suitable host.

While it is impossible to say conclusively that this patient was harboring some specimens of this parasite it is extremely probable that he was in fact doing so.

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